

MAPPED PERMANENT QUADRATS: A WINDOW THROUGH TIME
INTO HERBACEOUS PLANT DEMOGRAPHY

By Helen E. Dowling

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Approved:

Margaret M. Moore, Ph.D., Chair

Robert T. Strahan, Ph.D.

Larissa L. Yocom Kent, Ph.D.

Bradley J. Butterfield, Ph.D.

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ABSTRACT

MAPPED PERMANENT QUADRATS: A WINDOW THROUGH TIME INTO HERBACEOUS PLANT DEMOGRAPHY

HELEN E. DOWLING

Long-term spatially explicit mapped datasets of herbaceous plant population dynamics are rare and intrinsically valuable beyond measure. These types of data can provide vital information to address key ecological questions related to plant demography, population and community responses to climate and anthropogenic modifications across the landscape. The long-term historical dataset, which is the focus of this thesis, provides examples of the ecological value of data derived from long-term permanent chart quadrats.

In Chapter 2, I provide metadata from a long-term dataset that consists of 98 permanent 1-m² quadrats located in the ponderosa pine-bunchgrass ecosystem surrounding Flagstaff, Arizona, USA. Individual plants in these quadrats were identified and mapped annually from 2002-2014. Original quadrats were established in 1912-1927 and were mapped sporadically until 1940. Quadrats were located in ungrazed exclosures and in pastures grazed at various intensities by livestock. I provide the following data and data formats: (1) high-resolution image files (*.tiff); (2) the digitized maps in shapefile format; (3) a tabular representation of centroid or point location (*x*, *y* coordinates), and basal cover for plants mapped as polygons; (4) a species list including the total records for each species; (5) quadrat inventory of the years each quadrat was sampled; (6) quadrat information including GPS coordinates and elevation; and (7) monthly

precipitation and temperature records. The metadata results (data products) will be published in research archives. In addition, data from these permanent chart quadrats will be used to determine species-specific vital rates in Chapter 4.

In Chapter 3, I developed an electronic field data collection method to remap the herbaceous vegetation on the chart quadrats described above. The method uses ESRI ArcMap to collect plant data on field computers, which: (1) creates a digital data capture system; (2) allows the ability to search and manipulate the data from directly in the field; (3) allows for a visual display of the previous year's data map for reference in the field; (4) reduces the likelihood of data transposition errors; and (5) removes the need to digitize maps from paper copies. I tested the electronic field data collection method against the traditional paper mapping method to assess the efficiency of each method. The electronic data collection method increased the amount of time necessary to map the vegetation on each quadrat, however, the electronic method significantly diminished the amount of time needed to process each quadrat in the office. Implementing the electronic method can reduce the amount of time and resources needed to annually re-map permanent chart quadrats.

In Chapter 4, I used detailed local climate variables and data from the annually remapped data set (2002-2014) described above to examine the effects of climate on the demographic rates of a dominant graminoid, Arizona fescue (*Festuca arizonica* Vasey). I constructed life tables to examine vital rates (e.g., survival probabilities, growth, and life expectancies) for this focal species. I made population projections using the species' state (size) and precipitation

variables using Integral Projection Models (IPMs) to quantify the direct influence of seasonal precipitation on the vital rates of this dominant perennial bunchgrass.

We found that altering the size structure of the population of Arizona fescue can increase life span by increasing the number of individuals belonging to the larger size classes with higher probabilities of survival. Furthermore, we found that the survival and growth of Arizona fescue was strongly linked with winter and spring precipitation, respectively.

In summary, in this thesis I compiled metadata from a historical dataset, developed an electronic field capture method, and used these data to examine the demographic rates of a dominant bunchgrass species in northern Arizona.

Gaining a better understanding of the climatic factors that drive plant populations will allow land managers to make informed decisions regarding land-use practices and the implementation of restoration treatments in the Southwest. In an era characterized by anthropogenic climate and land-use change, understanding the impacts these changes may have on forest ecosystems is crucial in our effort to anticipate how plant communities may respond over time.

ACKNOWLEDGMENTS

I would like to thank my committee chair, Dr. Margaret M. Moore, and my committee members Dr. Robert T. Strahan, Dr. Larissa L. Yocom Kent, and Dr. Bradley J. Butterfield for their guidance and support throughout the research process. I want to give a special thank you to Dr. Strahan, who helped guide me through the details of Integral Projection Models. I would also like to thank Dr. Jonathan D. Bakker, Dr. Daniel C. Laughlin, and Dr. Robert T. Strahan, who helped relocate, remap and digitize these original chart quadrats between 2002-2014; this project would not have been possible without their previous efforts. I also thank Ian Fox and Carol Finoti for the many hours spent in the lab and in the field.

I would like to thank the Coconino National Forest and USDA Forest Service Rocky Mountain Research Station (RMRS; Fort Valley Experimental Forest, FVEF) for allowing me to sample data on their lands, especially Susan D. Olberding for assisting with records in the FVEF Archives. Finally, I would like to thank the Northern Arizona University (NAU) Ecological Restoration Institute (ERI) for their support in the annual field mapping and digitizing of these historical chart quadrats, and computer support of the long-term databases. I would like to thank the Statistical Consultation Lab at NAU for their contributions. Partial funding was provided by the Support for Graduate Students Grant Program administered by the NAU Applied Research and Development and the NAU School of Forestry.

Helen E. Dowling

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PREFACE

This thesis is presented in journal format and consists of three manuscript chapters, which will be submitted for publication in scientific journals.

Redundancy among these chapters is due to the overlap in methodology, data, and authors. The three data chapters will involve co-authors, therefore the collective pronoun “we” is used instead of “I”. Chapters 2 and 4 will be submitted to the journal *Ecology*, while Chapter 3 will be submitted to *Rangeland Ecology and Management* as a Technical Note.

CHAPTER 1: INTRODUCTION

Understanding how plant population dynamics are influenced by climate variation is a classic ecological inquiry that has taken on a new level of urgency in an era of anthropogenic climate and land-use change (Dalglish et al. 2011, Adler et al. 2012, Chu et al. 2014). The future of ecosystem conservation and management will rely on our ability to accurately forecast the ecological impact of these changes and predict species interactions and community level responses over time (Adler et al. 2012).

Since Euro-American settlement, fire suppression and grazing practices have significantly increased tree densities in southwestern ponderosa pine (*Pinus ponderosa* Laws. var. *scopolorum* Engelm.) dominated forests. Figure 1.1 illustrates the dramatic divergence between current forest structure and the forest structure that was characteristic of pre-settlement southwestern ponderosa pine forests. Time series photos (Fig. 1.1) document the effects of anthropogenic modifications (i.e., grazing, fire suppression) that are present throughout our entire study area. This shift in forest structure coupled with the absence of fire has profoundly impacted the herbaceous understory in these formerly frequent-fire ecosystems (Covington and Moore 1994a, 1994b). Many studies have addressed the impacts of anthropogenic modifications on plant communities; however, few studies have addressed the impact of climate change on herbaceous plant population dynamics.

Understanding how communities have responded to past climatic variation provides a method of predicting community level responses to future climate

change (Dalglish et al. 2011). Fluctuations in temperature and precipitation common in the American Southwest are predicted to increase and have the potential to disrupt plant life cycles (Lenart et al. 2007). Projections based on the results of 19 global climate models suggest that the Southwest's immediate future will likely resemble the severe drought of 2002 and possibly last for many consecutive years (Lenart et al. 2007). It is evident that plant species have responded differently to recent shifts in climate, yet how they may respond to future climate change remains unknown.

Our ability to accurately predict plant population dynamics is hindered in part by a lack of empirical demographic data (Lauenroth and Adler 2008). For the majority of plant species in the Southwest, data pertaining to population demographic rates remains unknown. Mapping individual plants over time is the most accurate method of determining demographic parameters for herbaceous plant species (Lauenroth and Adler 2008). In this thesis, I used a long-term data set from within the ponderosa pine-bunchgrass ecosystem of the Southwest that contains the best data available to investigate the demography of a dominant perennial bunchgrass. This network of fine-grained (1-m²) permanent plots was remeasured annually from 2002-2014, for a total of 13 consecutive years. These chart quadrats were originally established by R. R. Hill, C.K. Cooperrider, H.O. Cassidy, and G.A. Pearson between 1912 and 1927 on the Coconino National Forest and Fort Valley Experimental Forest. They provide a unique opportunity to examine the influence of climate change on the demography of plant

populations in the southwestern ponderosa pine bunchgrass ecosystem (Bakker and Moore 2007, Bakker et al. 2008, Laughlin et al. 2009, Strahan et al. 2015).

The objectives of my thesis were to: (1) continue the annual mapping of these permanent quadrats and further contribute to this scientific legacy; (2) maintain and prepare this large and valuable ecological dataset for publication in *Ecological Archives* (Chapter 2); (3) develop digital methods for more efficient field data collection and entry of chart quadrat data (Chapter 3); (4) determine the demographic rates (e.g., survival, growth, and life expectancy) of Arizona fescue, a dominant graminoid species (Chapter 4); and (5) quantify the direct influence of seasonal precipitation using an Integral Projection Model (IPM) (Chapter 4). My goal is to provide a better understanding of the climatic factors that drive plant species populations on so that land managers can make informed decisions regarding land-use practices in the Southwest and in the implementation of restoration treatments across the landscape.

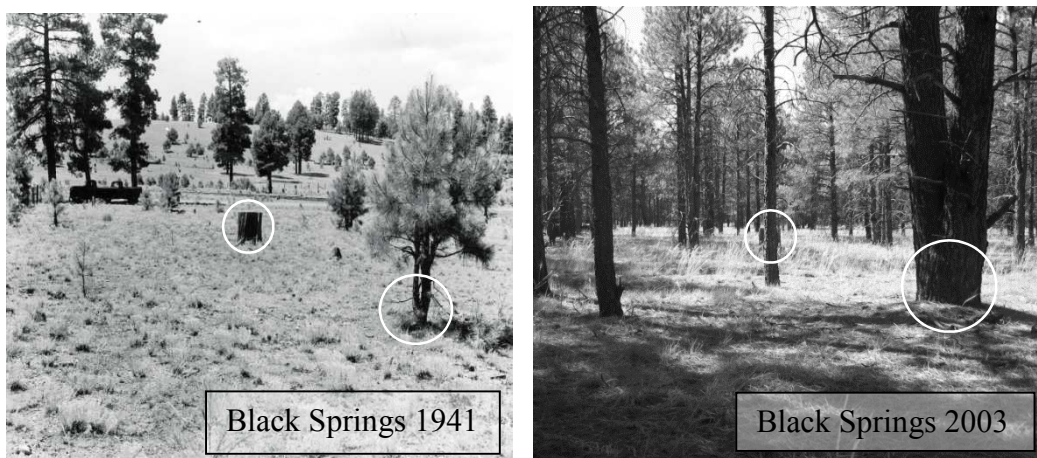


Figure 1.1. Photographs illustrating the divergence in forest structure that has occurred in southwestern ponderosa pine forests; white circles highlight the same stump and tree in both photos. Photographs from 1941 (left) and 2003 (right) are of the area outside the grazing exclosure at the Black Springs site. The 1941 photo was taken by G. Glendening (US Forest Service photo 421124), and the 2003 photo was taken by J.D. Bakker (Bakker 2005, Bakker et al. 2008).

CHAPTER 2:
MAPPED CHART QUADRATS IN SOUTHWESTERN PONDEROSA PINE-
BUNCHGRASS ECOSYSTEMS: LONG-TERM DATA FOR ANALYZING
HERBACEOUS PLANT DYNAMICS

Abstract

This historical data set consists of a series of 98 permanent 1-m² chart quadrats from within the ponderosa pine-bunchgrass ecosystems of northern Arizona, USA. We relocated these chart quadrats and remapped all individual plants in each quadrat annually from 2002-2014. The temporal and spatial data provide unique opportunities to examine the effects of climate and land-use variables on plant demography, population and community processes. The original chart quadrats were established between 1912 and 1927 to determine the effects of livestock grazing on herbaceous plants and pine seedlings. We briefly describe the three distinct historical studies that led to the establishment of this larger network of 98 permanent quadrats.

We provide the following data and data formats: (1) high-resolution image files (*.tiff); (2) the digitized maps in shapefile format; (3) a tabular representation of centroid or point location (x, y coordinates); and basal cover for species mapped as polygons; (4) a species list including the total records for each species, (5) quadrat inventory of the years each quadrat was sampled; (6) quadrat information including GPS coordinates and elevation; and (7) monthly precipitation and temperature records.

Introduction

Our ability to accurately predict plant population dynamics is hindered in part by a lack of empirical demographic data (Laurenroth and Adler 2008). For the majority of the herbaceous plant species in the Southwest, data pertaining to demographic rates and population dynamics is virtually unknown. Mapping individual plants over time is the most accurate method of determining demographic parameters for herbaceous plant species (Laurenroth and Adler 2008). These temporal and spatial data derived from mapped chart quadrats provide unique opportunities to examine the effects of climate and land-use variables on plant demography, population, and community processes.

Mapped chart quadrats were originally designed and popularized by Clements (1905) to assess the composition and structure of plant communities. Networks of chart quadrats were widely established in the western U.S. rangelands in the 1900s. They are fine-grained permanent quadrats and maps showing the location of individual plants. In the past, chart quadrat data have been used to analyze plant demography (Albertson and Tomanek 1965, Laurenroth and Adler 2008), and there is a renewed interest in relocating and remapping permanent chart quadrats because of their tremendous importance for ecological theory (Adler et al 2006,), vegetation response to climate change (Adler et al 2012, Yao et al 2006), soil processes (Gill 2007), and questions regarding bet hedging (Gremmer and Veneable 2014), and biodiversity (Adler and Laurenroth 2003, White et al. 2006, Adler and Levine 2007). Much of what

we know about demographics, population, and community dynamics of herbaceous plants in the Southwest has come from chart quadrats such as these.

The chart quadrats that are the foci of this metadata consists of a series of 98 permanent 1-m² chart quadrats from within the ponderosa pine-bunchgrass ecosystems in northern Arizona, USA. All of these quadrats are located within 40 km of Flagstaff, AZ (Figure 2.1) and are distributed over multiple sites spanning 700 km² of varying soil type, topography, and spanning the elevational range of the ponderosa pine-bunchgrass type on the Coconino National Forest and Fort Valley Experimental Forest in northern Arizona (Bakker and Moore 2007, Laughlin et al. 2011, Strahan et al. 2015). The precise locations of corners and boundaries for ninety-eight quadrats remain permanently marked (tagged angle iron or galvanized steel pipe corners) in the field. During each growing season, all plants found on these quadrats are identified, remapped, and digitized into geographic information systems to facilitate calculations of individual plant and total basal cover and density (Laughlin and Moore 2008).

Original Chart Quadrats from Three Historical Studies

The chart quadrats archived in this database were originally established by R.R. Hill, C.K. Cooperrider, H.O. Cassidy, and G.A. Pearson between 1912 and 1927 on the Coconino National Forest and Fort Valley Experimental Forest. Initially established to examine: (1) the effects of grazing on the herbaceous plant community, (2) grass competition with pine seedling establishment, and (3) initial patterns of plant succession. We provide a brief description, background and literature for each study. The original hand drawn chart quadrat maps, plus

original photographs and the summaries from all three studies, are stored in the FVEF Archives at the Rocky Mountain Research Station (RMRS) in Flagstaff (<http://www.rmrs.nau.edu/fortvalley>).

R. R. Hill became the first United States Forest Service (USFS) Grazing Examiner for District 3 (now Region 3) in 1908. He initiated a study on the Coconino National Forest to examine potential livestock damage to ponderosa pine (*Pinus ponderosa* Laws. var. *scopolorum* Engelm.) regeneration as well as determine how the understory vegetation recovers when protected from livestock grazing in 1912 (Hill 1917, Hill 1920, Talbot and Hill 1923, Glendening 1941, Arnold 1950, Arnold 1955, Bakker 2005, Bakker et al. 2008). Under Hill's direction, livestock exclosures (0.6 ha) were built at 5 sites on the Coconino National Forest. At each site, 10 1-m² chart quadrats were established, five inside and five outside the exclosures. Vegetation on these 50 chart quadrats was mapped periodically between 1912 and 1948 before the project ended and their data archived at the Fort Valley Experimental Forest. This study is known locally as the "Hill Plots" in recognition of R.R. Hill and these quadrats have been mapped annually since 2002 (Bakker 2005, Bakker et al. 2008, Laughlin 2009, Laughlin et al 2011, Strahan 2013, Strahan et al. 2015) and are labelled according to their site name, such as "Black Springs", "Rogers Lake", etc.

In 1909, G. A. Pearson, Director, USFS Fort Valley Experimental Forest (FVEF), together with T.S. Woolsey Jr. drafted a set of instructions that led to the establishment of a network of permanent sample silvicultural plots (PSP) in the ponderosa pine forests of the Southwest (Pearson 1923, 1933, 1942, Moore et al.

2004). On the PSPs that are located on the FVEF, there are a set of nested understory subplots, which were established in 1914 to quantify woody and herbaceous plant composition, and secondary plant succession. The nested understory plots were 1.5 x 3.0 m and were permanently marked with iron pipes (Moore et al. 1999, Bakker et al. 2002). We have annually remapped 10 1-m² quadrats within these original understory plots since 2006 (Laughlin 2009, Laughlin et al. 2011, Strahan 2013), and these quadrats are labelled according to their FVEF PSP name, such as S1A, S2A, S3A, etc.

In 1927, the FVEF initiated a study on the Wild Bill range of the Coconino National Forest to experimentally isolate the agents responsible for injury to ponderosa pine regeneration (Cooperrider 1938, 1939), while simultaneously assessing the impacts of livestock grazing on herbaceous composition and cover through the establishment of chart quadrats (Laughlin and Moore 2008). Known as the “Cooperrider-Cassidy Range Study”, quadrats were installed on the USFS range allotments which covered ~12,000 ha northwest of Flagstaff, Arizona, known as the Wild Bill and Willaha (Cooperrider and Cassidy 1939a, 1939b, Laughlin and Moore 2008). We have annually remapped these 28 1-m² quadrats since 2006 (Laughlin 2009, Laughlin et al. 2011, Strahan 2013, Strahan et al. 2015) and these plots are labelled as “Wild Bill” in the database.

We provide the following data and data formats: (1) high-resolution image files (*.tiff); (2) the digitized maps in shapefile format; (3) a tabular representation of centroid or point location (x, y coordinates); and basal cover for species mapped as polygons; (4) a species list including the total records for each

species, (5) quadrat inventory of the years each quadrat was sampled; (6) quadrat information including GPS coordinates and elevation; and (7) monthly precipitation and temperature records.

Metadata Description

CLASS I. DATA SET DESCRIPTORS

Data set identity: Mapped plant community time series, Flagstaff, AZ, 2002-2014

B. Data set identification code: Not applicable (N/A)

C. Data set description

1. Principal Investigators:

Margaret M. Moore, Professor, School of Forestry, Northern Arizona University,
Flagstaff, AZ, 86011, USA

Robert T. Strahan, Postdoctoral Scholar, Ecological Restoration Institute,
Northern Arizona University, Flagstaff, AZ, 86011, USA

Helen E. Dowling, Graduate Research Assistant, School of Forestry, Northern
Arizona University, Flagstaff, AZ, 86011, USA

Jonathan D. Bakker. Associate Professor, School of Environmental and Forest
Sciences, University of Washington, Seattle, WA, 98195

Daniel C. Laughlin, Assistant Professor, Environmental Research Institute and
Department of Biological Sciences, University of Waikato, Hamilton, NZ

2. Abstract: See Chapter 2 Abstract (above).

CLASS II. RESEARCH ORIGIN DESCRIPTORS

A. Overall project description: We relocated, remapped, and digitized the
vegetation on these historical chart quadrats in ArcGIS.

B. Specific subproject description

1. Site description: All permanent quadrats are located within 40 km of Flagstaff, AZ, and are distributed over multiple sites spanning 700 km² of varying soil type, topography, and spanning the elevational range of the ponderosa pine-bunchgrass ecosystem type of northern Arizona

a. Site type: N/A

b. Geography: The study site is located within 700 km² of Flagstaff, Arizona, on the Coconino National Forest and Fort Valley Experimental Forest between the elevations of 2,000-2,500 m. Soil types are derived from basalt, limestone, and sandstone parent materials.

c. Habitat: Arnold (1950), Pearson (1950), Covington and Moore (1994 *a* and *b*), Bakker (2005), Bakker and Moore (2007), Bakker et al. (2008), Laughlin and Moore (2008), Laughlin et al. (2011), and Strahan et al. (2015) describe the vegetation at these sites. The vegetation type is characteristic of the ponderosa pine-bunchgrass ecosystem, though the cover of herbaceous vegetation is often sparse in areas with high ponderosa pine tree canopy cover. In these areas, high loads of down woody debris (i.e., litter and duff) are interspersed with numerous patches of bare ground and exposed rock. The most conspicuous woody components of the vegetation where the quadrats are located are trees, shrubs and subshrubs. Overstory trees are primarily comprised of the two native tree species ponderosa pine (*Pinus ponderosa* Laws. var. *scopularum* Engelm.) and Gambel oak (*Quercus gambelii* Nutt. Var. *bonina* S.L. Welsh); and several juniper species (*Juniperus spp.*) are present at the Big Fill site. There are many native shrub and

subshrub species that occur in close proximity to these quadrats, the shrubs and subshrubs that have been mapped on these quadrats include: three-leaf sumac (*Rhus trilobata* Nutt.), Woods' rose (*Rosa woodsii* Lindl. Var. *glabrata* (Parish) Cole), and broom snakeweed (*Gutierrezia sarothrae* (DC.) A. Gray). The understory herbaceous plant community is the major source of plant biodiversity in these ecosystems and is dominated by perennial bunchgrasses followed by perennial forbs and annual and biennial forbs. In the meadows and forested openings are the forbs, grasses and graminoids. Grasses and graminoids primarily include: Arizona fescue (*Festuca arizonica* Vasey), mountain muhly (*Muhlenbergia montana* (Nutt.) A.S. Hitchc.), squirreltail (*Elymus elymoides* (Raf.) Swezey), upland sedge (*Carex sp.*), muttongrass (*Poa fendleriana* (Steud.) Vasey ssp. *albescens* (Hitchc.) Soreng), pine dropseed (*Blepharoneuron tricholepis* (Torr.) Nash), black dropseed (*Sporobolus interruptus* Vasey) (endemic to northern Arizona), and Kentucky bluegrass (*Poa pratensis* L. ssp. *alpigena* (Fr. ex Blytt) Hiitonen). The forbs are diverse and less uniform in their distribution, several of the most widely abundant forb species include: common yarrow (*Achillea millefolium* L. var. *alpicola* (Rydb.) Garrett), Carruth's sagewort (*Artemisia carruthii* Alph. Wood ex Carruth), Kaibab pussytoes (*Antennaria rosulata* Rydb.), fetid goosefoot (*Chenopodium graveolens*), thymeleaf sandmat (*Chamaesyce serpyllifolia* Pers.), trailing fleabane (*Erigeron flagellaris* A. Gray), spreading fleabane (*Erigeron divergens* Torr. & A. Gray), and western aster (*Symphyotrichum ascendens* Lindl. G.L. Nesom).

- d. Geology: The study area spans the range of soil types developed from basalt, limestone, and sandstone parent materials (Bakker 2005, Laughlin 2009, Strahan 2013).
- e. Watersheds/hydrology: Throughout the entire study area there is an absence of surface water except for the Rogers Lake site which is in close proximity to the large natural wetland area known as Rogers Lake, an ephemeral stream that occurs in close proximity to the Black Springs site, and a man-made tank in close proximity to Reese Tank.
- f. Site history: The 10 quadrats, which are permanent sample plots (PSP) (such as S1A, S2A, S3A, etc.), are located either within the Fort Valley Experimental Forest (FVEF) in close proximity to Highway 180. There are no grazing enclosures associated with these quadrats. The 50 quadrats known as the “Hill Plots” are distributed at 5 distinct sites each of which contains a grazing enclosure: (1) Big Fill is located across from a ranch house on Old Walnut Canyon Road (FS road 303) about 3.2 km southeast of junction with Country Club Drive, (2) Black Springs is located on Old Mund’s Highway (FS road 762) 1.2 km southeast of junction with Highway 89A and directly west of Interstate 17; (3) Fry Park is located in the northwest corner of Fry Park along FS road 535; (4) Reese Tank is bisected by FS road 418 and southwest of Bearjaw Fire on the north side of the San Francisco Peaks; and (5) Rogers Lake is located at the junction of Woody Mountain Road (FS road 231) and road to Aspen Spring Ranch 0.8 km south of Rogers Lake. The 28 quadrats known as the “Wild Bill Plots” are dispersed widely throughout the Wild Bill and Willaha grazing

allotments that are located west and northwest of the San Francisco Peaks and to the south or at the base of Kendrick Mountain.

g. Climate: Mean annual precipitation is 565 mm and mean annual temperature is 7.7°C (Kohn and Welker 2005, Strahan 2013). G.A. Pearson (1931) provides a thorough description of the climate in northern Arizona, further information pertaining to contemporary climate description was through the Western Regional Climate Center (WRCC) (<http://www.wrcc.dri.edu/narratives/ARIZONA.htm>), through NOAA (<https://www.ncdc.noaa.gov/data-access/land-based-station-data>) for the Pullman Airport weather station, and the USFS RMRS FVEF climate data catalog (<http://www.fs.fed.us/rm/fort-valley/data/>). Annual means in precipitation fluctuate more widely than temperature for in northern Arizona. Daily or monthly mean temperature exhibit greater fluctuations than averages are for periods of a year or longer. The daily range between maximum and minimum temperature can be as large as 50 to 60 degrees between day time high and night time low, however, mean annual temperatures seldom fluctuate more than 10 percent versus precipitation averages that often fluctuate as much as 100 percent. Growing season is, on average, less than 3 months but can begin as early as April and persist through October (WRCC). Periodic droughts are common in northern Arizona and tend to occur when mean monthly temperature and precipitation are at their lowest. Great yearly and periodic variation in precipitation is characteristic of northern Arizona and present throughout our study area, precipitation patterns for this region are bimodal and occur in the winter and summer months (WRCC). Precipitation is governed by elevation and season of

the year. From November through March, winter storms bring snow which can accumulate to depths of 2,540 mm or more (WRCC). The gradual melting of snow during the spring is important source of water to maintain soil moisture, especially during the late spring and early summer when rainless periods are common. Summer rainfall occurs in the form of thunderstorms (referred to as the summer monsoons) which begin early in July and usually lasts until mid-September (Pearson 1931).

2. Experimental or sampling design

a. Design characteristics:

1. "Fort Valley Experimental Forest - PSP" are comprised of 10 permanent chart quadrats, none of which are contained in a grazing enclosure.
2. "Hill Plots" are comprised of 50 permanent chart quadrats distributed at 5 sites. At each site there are a total of 10 quadrats, five inside a grazing enclosure and five outside the grazing enclosure.
3. "Wild Bill Plots" are comprised of 28 permanent chart quadrats dispersed throughout two grazing allotments. (Wild Bill and Willaha).

b. Permanent plots: See quadrat information data file in IV.

c. Data collection:

All quadrats are mapped during the late summer, typically during a 4 week period in August.

1. "FVEF PSP" were mapped in 1914 and again in 1919, and have been remapped annually since 2006.

2. “Hill Plots” were mapped periodically from 1912 until 1948, and have been remapped annually since 2002.
3. Wild Bill plots” Quadrats were mapped annually from 1927 through 1938, and have been remapped annually since 2006.

3. Research Methods

- a. Field / laboratory: Historical data were collected in the field using pantographs (Hill 1920), a mechanical device used to make scale drawings. Contemporary data are collected in the field using a PVC chart quadrat that is further subdivided into a grid with 25 cells. Each cell is mapped onto a transparency sheet with a grid system that is transcribed onto a paper data sheet. The original paper maps (both historical and contemporary) are first scanned and then stored as TIFF image files. These images are then uploaded as raster images in ArcMap where each individual plant is digitized into shapefiles in ArcGIS. For a complete digitization protocol, contact Margaret M. Moore. Monthly climate data was obtained from the USFS RMRS FVEF climate data catalog (<http://www.fs.fed.us/rm/fort-valley/data/>) and through NOAA (<https://www.ncdc.noaa.gov/data-access/land-based-station-data>) for the Pullman Airport weather station
- b. Instrumentation: Pantographs (historical), paper data sheets (contemporary), scanners, and computers running ArcGIS, Python, and R.
- c. Taxonomy and systematics: Originally assigned plant names were corrected for synonyms, and historical and contemporary names resolved (Bakker 2005,

Laughlin 2009). Current names are based on the USDA Plants Database (<http://plants.usda.gov/>).

d. Permit history: Permits were obtained through the Coconino National Forest and the Fort Valley Experimental Forest.

e. Legal / organizational requirements: None.

CLASS III. DATA SET STATUS AND ACCESSIBILITY

A. Status

1. Latest Update: December 2014.

2. Latest Archive date: December 2014.

3. Metadata status: The metadata are complete and up to date.

4. Data verification: All maps are checked for completeness and accuracy initially after all individuals have been digitized again prior to spatial adjustment. Helen

E. Dowling made the following changes to the original (digitized) GIS dataset (stored shapefiles) between 2013 and 2014: (1) Shapefiles were rotated to have a consistent North-South vertical orientation; (2) Species names for large unlabeled or obviously mislabeled polygons were assigned based on species names assigned to the same features in previous or later years; (3) Shapefiles were processed using R and Python scripts to cut polygons and point features at the map borders and remove any small polygon “slivers” generated accidentally while digitizing; (4) Other miscellaneous corrections based on visual inspection of the shapefiles; (5) All species were then classified as either density- or cover-type features. All grasses and graminoids are digitized as polygon features. All woody (tree and shrub) and forbs, with the exception of three species, are digitized as point

features; (6) Plant names were corrected for synonyms based on the USDA PLANTS Database (<http://plants.usda.gov/>). Some questionable, infrequent taxa lumped into "sp." categories; and (7) x, y coordinates of each polygon centroid were added to shapefile attribute tables.

B. Accessibility

1. Storage location and medium: The data are available from the Ecological Society of America's data archives. Duplicate copies of the data are being stored along with supplementary data associated with this data set at the RMRS USFS FVEF (<http://www.rmrs.nau.edu/fortvalley>). Data will be entered into the US Forest Service Research Archive Repository.

2. Contact person: Margaret M. Moore, School of Forestry, Northern Arizona University, Flagstaff, AZ, 86011 USA, Margaret.Moore@nau.edu

3. Copyright restrictions: None.

4. Proprietary restrictions: None.

5. Costs: None.

CLASS IV. DATA STRUCTURAL DESCRIPTORS

SPATIAL DATA

A. Data Set File

1. Identity: shapefiles.zip

2. Size: 2,141,960 bytes.

3. Format and storage mode: Shapefiles compressed and submitted together in a zipped directory.

4. Header information: The fields within the attribute tables for each shapefile are

described in the tabular data, see "All records density" for records of all individual plants mapped as points and "All record cover" for records of all individual plants mapped as polygons.

B. Variable information: This is a zipped directory, containing a series of subdirectories, each corresponding to one quadrat. Within the subdirectories are individual shapefiles for each year that the quadrat was mapped. File names reflect the quadrat (quad), year, and geometry (C or D) of each shapefile. C refers to "cover" while D refers to "density". Features in cover files (grasses, graminoids, and three forb species) are mapped as polygons, while features in density files (forbs, shrubs, single blade grass individuals, and pine seedlings) are mapped as points. Each feature in these shapefiles has attributes that describe the individual, such as species name and location within the quadrat. The size of this zip file is 2,092 KB.

RECORDS OF ALL INDIVIDUAL PLANTS MAPPED AS POINTS

A. Data Set File

1. Identity: allrecords_density.csv
2. Size: 40,894 records, 3,466,014 bytes.
3. Format and storage mode: ASCII text, comma separated. No compression scheme was used.
4. Header information: The first row of the file contains the variable names below.

B. Variable information: See Table 2.1.

RECORDS OF ALL INDIVIDUAL PLANTS MAPPED AS POLYGONS

A. Data Set File

1. Identity: allrecords_cover.csv
2. Size: 106,638 records, 5,943,591 bytes.
3. Format and storage mode: ASCII text, comma separated. No compression scheme was used.
4. Header information: The first row of the file contains the variable names below.

B. Variable information: See Table 2.2.

QUADRAT INFORMATION

A. Data Set File

1. Identity: quad_info.csv
2. Size: 98 records, 1,491 bytes.
3. Format and storage mode: ASCII text, comma separated. No compression scheme was used.
4. Header information: The first row of the file contains the variable names below.

B. Variable information: See Table 2.3.

QUADRAT SAMPLING SCHEDULE

A. Data Set File

1. Identity: quad_inventory.csv
2. Size: 14 records, 6,389 bytes.

3. Format and storage mode: ASCII text, comma separated. No compression scheme was used.

4. Header information: The first row of the file contains the variable names below.

B. Variable information: See Table 2.4.

SPECIES LIST FOR SPECIES MAPPED AS POINTS

A. Data Set File

1. Identity: species_list_density.csv

2. Size: 237 records, 5,597 bytes.

3. Format and storage mode: ASCII text, comma separated. No compression scheme was used.

4. Header information: The first row of the file contains the variable names below.

B. Variable information: See Table 2.5.

SPECIES LIST FOR SPECIES MAPPED AS POLYGONS

A. Data Set File

1. Identity: species_list.csv

2. Size: 60 records, 1,501 bytes.

3. Format and storage mode: ASCII text, comma separated. No compression scheme was used.

4. Header information: The first row of the file contains the variable names below.

B. Variable information: See Table 2.6.

MONTHLY TEMPERATURES

A. Data Set File

1. Identity: monthly_mean_temp.csv
2. Size: 14 records, 948 bytes.
3. Format and storage mode: ASCII text, comma separated. No compression scheme was used.
4. Header information: The first row of the file contains the variable names below.

B. Variable information: See Table 2.7.

MONTHLY PRECIPITATION

A. Data Set File

1. Identity: total_monthly_ppt.csv
2. Size: 14 records, 950 bytes.
3. Format and storage mode: ASCII text, comma separated. No compression scheme was used.
4. Header information: The first row of the file contains the variable names below.

B. Variable information: See Table 2.8.

CLASS V. SUPPLEMENTAL DESCRIPTORS

A. Data acquisition

1. Data forms: N/A

2. Location of completed data forms: The original chart quadrat data sheets are archived at the Fort Valley Experimental Forest Archives

(<http://www.rmrs.nau.edu/fortvalley>).

3. Data entry verification procedures: See II.3.

B. Quality assurance/quality control procedures: The procedures described above (II.3) ensured accurate transfer of information from the original to the digital maps and correction of some errors introduced at the original mapping stage.

Nevertheless, future users must become familiar enough with the raw data provided here to determine whether or not it is appropriate for their particular research question.

C. Related materials: Zip files containing the scanned images of the original maps (TIFF format, *.tiff) may be found at the School of Forestry, Northern Arizona University; contact person: Margaret M. Moore (see IIIB for contact information)

D. Computer programs and data processing algorithms: N/A

E. Archiving

1. Archival Procedures: Data files and associated metadata have been archived in the Fort Valley Experimental Forest Archives. The current link for the metadata is (<http://www.rmrs.nau.edu/fortvalley>).

2. Redundant Archival Sites: Data can also be accessed through the School of Forestry, Northern Arizona University; contact person: Margaret M. Moore (see IIIB for contact information) and US Forest Service Research Archive Repository.

F. Publications and results: subset the literature cited (can create a subset of literature cited from past publications using this dataset, this would be included in the literature cited section prior to submission for publication)

G. History of data set usage

1. Data request history: N/A

2. Data set update history: N/A

3. Review history: N/A

4. Questions and comments from secondary users: N/A

Table 2.1. Records of all individual plants mapped as points.

Variable Name(s)	Variable Definition	Unit/Format	Storage Type	Precision	Variable codes and definitions
quad	Name of quadrat	N/A	Character	N/A	N/A
year	The year of the observation	YYYY	Integer	1	N/A
Species	Latin name of the plant species, otherwise labelled “unknown”	N/A	Character	N/A	N/A
Seedling	Indicated whether an individual was mapped as a seedling.	N/A	Character	N/A	N: Age/stage of the individual is unknown Y: The individual is a seedling
x	Location of the record in the East-West direction of the quadrat	m	Fixed point	1.00E-015	N/A
y	Location of the record in the East-West direction of the quadrat	m	Fixed point	1.00E-015	N/A

Table 2.2. Records of all individuals mapped as polygons.

Variable Name(s)	Variable Definition	Unit/ Format	Storage Type	Precision	Variable codes and definitions
Quad	Name of quadrat	N/A	Character	N/A	N/A
year	The year of the observation	YYYY	Integer	1	N/A
Species	Latin name of the plant species, otherwise labelled “unknown”	N/A	Character	N/A	N/A
Area	Area of individual polygons	m ²	Fixed Point	1.00E-015	N/A
x	Location of the record in the East-West direction of the quadrat	m	Fixed point	1.00E-015	N/A
y	Location of the record in the East-West direction of the quadrat	m	Fixed point	1.00E-015	N/A

Table 2.3. Quadrat information.

Variable Name(s)	Variable Definition	Unit/Format	Storage Type	Precision	Variable codes and definitions
QuadName	Original quadrat name that is found on the original quadrat tag in the field and is a combination of site initials and unique number (ex. BF11999 is Big Fill site; quadrat 11999)	N/A	Character	N/A	N/A
Quad	Quadrat name for shapefiles which corresponds with quadrat number found in geodatabase (ex. Q28)	N/A	Character	N/A	N/A
Grazing	Presence or absence of grazing activities	N/A	Character	N/A	No: No grazing (quadrat is located inside livestock enclosure) Yes: Grazing present (quadrat is located outside of grazing enclosure)

Table 2.4. Quadrat inventory.

Variable Name(s)	Variable Definition	Unit/Format	Storage Type	Precision	Variable codes and definitions
Year	The year of the observation	YY	Integer	1	N/A
Quad (Q1, Q2, Q3 etc. See Quadrat Information data file for complete list)	Year values indicate that the named quadrat was sampled that year. NAs indicate that the named quadrat was not sampled in the specified year	YY	Integer	1	See variable definition

Table 2.5. Species list for all plant species mapped as points.

Variable Name(s)	Variable Definition	Unit/Format	Storage Type	Precision	Variable codes and definitions
species	Latin name of a plant species (<i>Genus, species</i>), and miscellaneous “unknown” labels	N/A	Character	N/A	N/A
records	The number of individual records of that species of plant	N/A	Integer	N/A	N/A

Table 2.6. Species list for all plant species mapped as polygons.

Variable Name(s)	Variable Definition	Unit/Format	Storage Type	Precision	Variable codes and definitions
species	Latin name of a plant species (<i>Genus, species</i>), and miscellaneous “unknown” labels	N/A	Character	N/A	N/A
records	The number of individual records of that species of plant	N/A	Integer	N/A	N/A

Table 2.7. Monthly temperatures.

Variable names(s)	Variable Definition	Unit/ Format	Storage type	Precision	Variable codes and Definitions
YEAR	Calendar year in which the temperatures were recorded	YYYY	Integer	N/A	N/A
JAN, FEB, MAR, APR, MAY, JUN, JUL, AUG, SEP, OCT, NOV, DEC, ANNUAL	Mean monthly temperature for that month, respectively	Fahrenheit	Floating Point	0.01	N/A

Table 2.8. Monthly precipitation.

Variable names(s)	Variable Definition	Unit/ Format	Storage type	Precision	Variable codes and Definitions
YEAR	Calendar year in which the precipitation measurements were recorded	YYYY	Integer	N/A	N/A
JAN, FEB, MAR, APR, MAY, JUN, JUL, AUG, SEP, OCT, NOV, DEC, ANNUAL	Total precipitation for that month, respectively	Inch	Floating Point	0.01	N/A

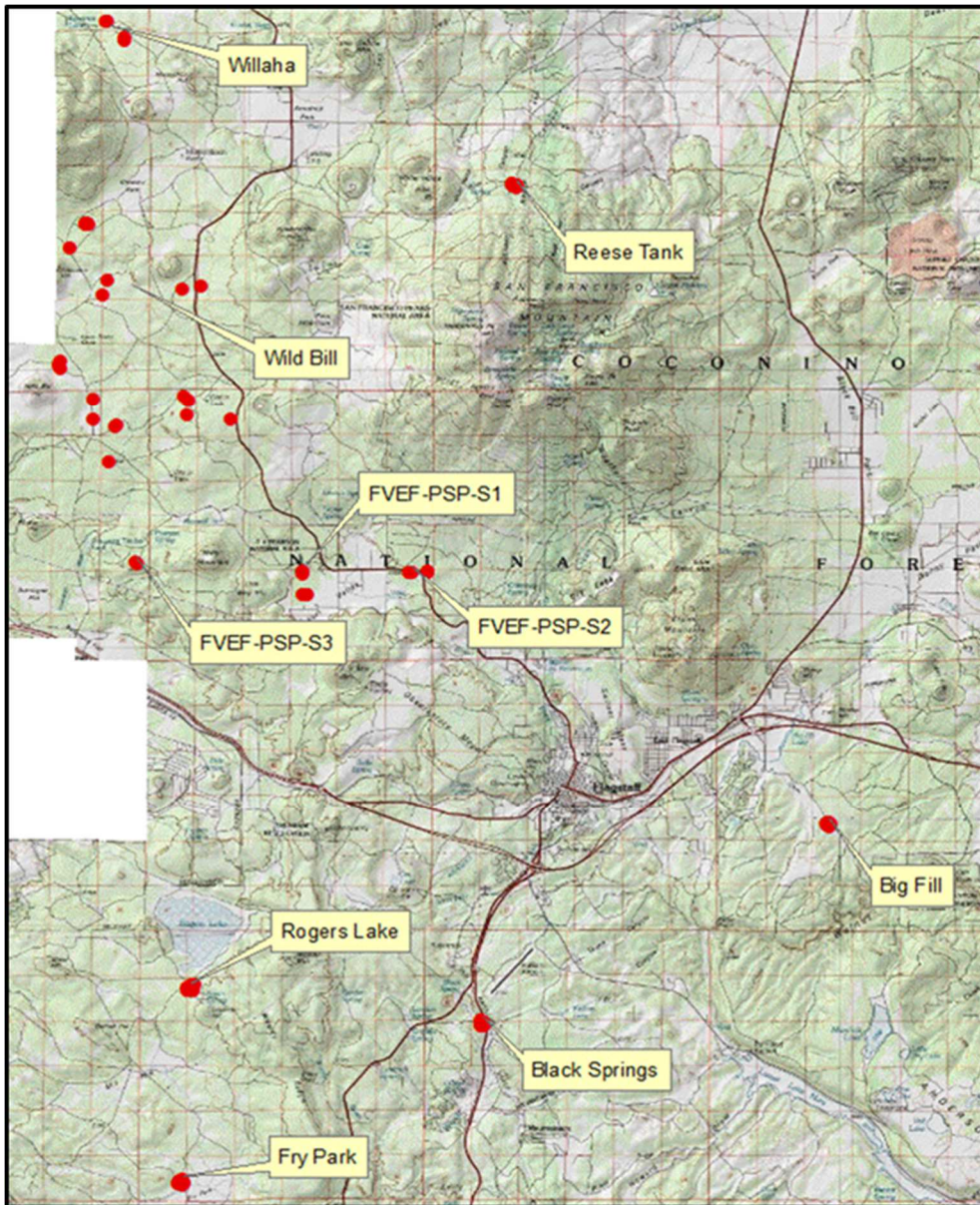


Figure 2.1. Study area map.

CHAPTER 3:
ELECTRONIC FIELD CAPTURE METHOD MORE EFFICIENT THAN
TRADITIONAL METHOD
FOR ANNUAL CENSUS OF HERBACEOUS PLANTS

Abstract

We developed an electronic field data collection method (electronic method) to remap the herbaceous vegetation on a set of 1-m² quadrats in the ponderosa pine-bunchgrass ecosystem in northern Arizona. The method uses ESRI ArcMap to collect plant data on field computers, which: (1) creates a digital data capture system; (2) allows the ability to search and manipulate the data from current and previous years; (3) allows a visual display of the previous year's data map while in the field; (4) reduces the likelihood of data collection errors; and (5) removes the need to digitize maps from paper copies. We tested the electronic data collection method against the traditional paper mapping method to assess the efficacy of these two methods. The electronic method increased the amount of field time necessary to map the vegetation on each quadrat, yet the amount of office time needed to process each quadrat was significantly diminished. In total (i.e., considering both field and office time), the electronic method eliminated an average of 26:49 (mm:ss) per quadrat. Implementing the electronic method can reduce the amount of time and resources needed to annually census the vegetation on permanent chart quadrats.

Introduction

The use of electronic field data capture methods in ecology has increased over the past few decades as technological advances allow new approaches to streamline data collection, processing, and dissemination efforts. Traditional paper-based field data collection procedures are both time and labor intensive. Limited funding available for field data collection has created an urgent need to streamline and develop more consistent methods using new GIS applications that will decrease the amount of time and labor necessary to complete field data collection for chart quadrat studies.

Computers are widely used in all aspects of ecological research but their application to in-field data collection for herbaceous understory vegetation has rarely been evaluated (Inman-Narahari et al. 2010). Previous studies have revealed other benefits associated with the development of new methods of digitizing data in the field. For example Buller and colleagues (2004) concluded that evolving from paper field notes to electronic field capture (field digitizing) has been shown to: (1) reduce the likelihood of transposition or scientific errors entering the data collection process; (2) increase our ability to search and manipulate the field data; (3) improve quality assurance and quality control from the inception of data collection; and (4) decrease the amount of time and labor needed to complete annual field data collection.

The primary purpose of this experiment was to assess the efficiency of the traditional paper-based method and the electronic field capture of data collection for fine-scaled herbaceous chart quadrats. To address this question, we developed

an electronic method using ArcGIS 10.2.2 that facilitates the electronic field capture of chart quadrat data with the use of a field computer (Panasonic Toughbook CF-191DYCX1M).

Methods

Study Area and Data Set

The study area, known as the Black Springs study site, is located 9.7 km south of Flagstaff, AZ in the ponderosa pine-bunchgrass ecosystem. This study site is part of the larger “Hill Plot” study (see Chapter 2, this thesis, Bakker and Moore 2007, Bakker et al. 2008, Laughlin et al. 2011, Strahan et al. 2015). The chart quadrats at this site were originally established in 1912 by R.R. Hill (Hill 1917, Talbot and Hill 1923). Ponderosa pine (*Pinus ponderosa* P. & C. Lawson var. *scopulorum* Englem.) is the only tree species present. The understory herbaceous vegetation is dominated by perennial grasses such as black dropseed (*Sporobolus interruptus* Vasey), muttongrass (*Poa fendleriana* (Steud.) Vasey), Arizona fescue (*Festuca arizonica* Vasey), and mountain muhly (*Muhlenbergia montana* (Nutt.) A.S. Hitchc.), along with a variety of forbs.

The Black Springs site contains 14 permanently marked 1-m² chart quadrats. The precise locations of corners and boundaries of chart quadrats are permanently marked (tagged angle iron or galvanized steel pipe corners) in the field. All herbaceous perennial vegetation in these quadrats are mapped and digitized into ArcMap (Figure 3.1).

We randomly selected a subset of 10 chart quadrats from the 14 quadrats at Black Springs. We mapped the perennial herbaceous vegetation (graminoids

and forbs) on the 10 quadrats using two methods, the traditional paper-based method (which has been used since 1912) and the newly developed electronic field data capture method. We used a stopwatch to time each step of each method both in the field and in the office. We recorded these times to assess the tradeoffs in time between the traditional paper-based and electronic data capture methods.

To randomize these data, we used a coin toss to determine which researcher would collect and which researcher would enter the data for each quadrat for each method. Figure 3.2 contains a work flow diagram illustrating the similarities and differences between the traditional paper-based method and the electronic data capture method. Data collection steps were completed in the field for both methods and were categorized under the “field time” for each method. Data entry steps were steps completed in the office for each method, and were categorized as “office time” in the analysis. There is a difference in the number of steps between the two methods due to: (1) the lack of the transcription step in the electronic data capture method; and (2) the additional scanning of paper data sheets to load as raster images in the traditional paper-based method.

Office Preparation

Prior to going into the field, for the traditional paper-based method, we prepared a field binder that included: a site map for Black Springs, the most recent data sheet for each selected chart quadrat, and 10 blank paper data sheets.

For the electronic field data capture method, we created point and polygon shapefiles for each quadrat and modified their attribute tables using the Visual Basic for Applications (VBA)/Macros function in ArcMap. We saved these pre-

made shapefiles into each quadrat subfolder with the corresponding Plot-specific Grid Template. We saved all subfolders into a site folder with site name and year in the title (i.e., BlackSprings_2014_IC), where IC indicates that data entry is incomplete. We saved the site folder onto the office computer, the field computer, and two separate USB drives so minimize the potential for lost data.

Chart Quadrat Method

Figure 3.2 contains a work flow diagram that illustrates the similarities and differences between the traditional paper-based method and the electronic field capture method of mapping chart quadrats. Both methods require that a 1-m² PVC sampling frame is overlain on top of the 1-m² chart quadrat in the field by orienting the frame precisely with the angle iron and rebar that permanently mark the corners of each quadrat. To do this consistently from year-to-year, symbols are included on each year's data sheet to illustrate the exact location of the rebar and angle iron in respect to the specific quadrat. Each year, the field crew orients the PVC frame using these angle iron/rebar symbols from previous year's data sheet for reference and the spatial location of the perennial plants within the quadrat.

The sampling frame is further divided into a grid of 25 cells (Fig. 3.3 right), each cell consisting of a smaller fine-grained grid. We printed 25 cells, each containing a fine-grain grid (Fig. 3.3, bolded), to allow the mapper to map each cell separately onto the corresponding grid transparency. This enabled the transcriber (traditional paper-based method) or digitizer (electronic data capture method) to map each individual to scale for each cell within the 1-m² chart

quadrat using the grid system. We mapped each chart quadrat using both methods. Again, a coin toss was used to determine which researcher would transcribe the data with each method.

The following descriptions highlight the differences between the two methods. The traditional paper-based method requires transcribing the 25 cells to scale on a paper data sheet using the fine-grained grid system to map each individual to scale based on its specific location within the quadrat (Fig. 3.3). These paper data sheets are then scanned and uploaded as raster images (resolution 1:4.214) in ArcMap so that each plant can be digitized as point or polygon features. The electronic field capture method eliminates the transcription step and allows the user to digitize the quadrat map directly from the 25 cells using the grid template to map each individual to scale, directly in the field.

For both methods, once each quadrat map is digitized, the corners of the square grid are spatially adjusted to a reference boundary that corresponds to one square unit of geospace. After the quadrat map has been spatially adjusted, the field calculator can be used to calculate the field geometry of each feature (individual plant) to determine the centroid or point location (x, y coordinates) and basal cover for species mapped as polygons. Since the units in the field calculator correspond to one square unit of geospace, and the chart quadrat is 1-m^2 , the area values for each polygon feature are given in cm^2 .

To facilitate electronic field capture, we developed a Grid Template using ArcMap 10.2.2 that replicated the square grid component of the paper data sheet that corresponds to the 1-m^2 chart quadrats. Initially, we tried to create the Grid

Template by replicating a grid from a raster image of a paper data sheet. Using the zoom function in ArcMap, we found that the cells on the paper data sheet were not of uniform size. Instead, we designed the grid template in ArcMap that consisted of uniform cells, which increased the spatial accuracy of each mapped individual by eliminating fine-scale discrepancies between cells.

To ensure that each quadrat is aligned correctly in the field, we included symbols at each corner of the grid to indicate the exact location of rebar and angle iron in respect to the quadrat. Once these plot-specific symbols were included in the Grid Template, we exported the Plot-Specific Grid Template as a TIFF file and saved it into the corresponding plot subfolder. We developed a Plot-Specific Information Template that included the component of the paper data sheet that contains a table for species mapped, percent cover estimates per species, and additional notes. We developed a Species List Template in Excel that consisted of a comprehensive list of the scientific names of all species recorded within the Black Springs study area.

Field Data Collection

In the field, for the traditional paper-based method, we transcribed each cell onto the paper data sheets with a mechanical pencil and used a metal tatum to prevent damage to the paper data sheets in the field. To maintain consistency with how the traditional method is employed during a normal field season, we began with the first cell in the first column (Fig. 3.3) and transcribed the entire column before moving on to the second column and so on until the final cell in the final column was completed. We drew in dots and angle symbols in reference

to the corners of the square grid component of the data sheet to illustrate the plot-specific location of the angle iron and rebar with respect to each chart quadrat.

These symbols ensure that the quadrat is properly aligned in the field. We listed all plant species in the species table and included the species symbols and percent cover estimates for each species.

In the field, for the electronic field data capture method, we used the construction tools in the editor function of ArcMap 10.2.2 to digitized perennial graminoid and several forb species as polygon features and the majority of forb species as point features. To increase efficiency, we digitized all individuals of the same species at the same time to enable us to copy and paste the species scientific names from the Species List Template into the attribute table using the field calculator. This reduces the potential for spelling errors and also saves time in the field. Once all species had been digitized, we saved our edits and exited ArcMap. We used the Plot-Specific Information Template to list all species in the species table and include percent cover estimates for each species. We saved the completed templates and shapefiles into the corresponding plot subfolders and transferred them into the site folder titled Black Springs_2014_C, where C indicates that data entry is complete. To minimize the risk of lost data, we saved the completed site folder onto the field computer and each USB drive in the field and transferred completed files to the office computer at the end of each field day.

Office Data Entry

For the traditional paper-based method, for steps that would typically be completed for several quadrats at one time (i.e., scanning data sheets into database

and making a folder connection in ArcCatalog), we recorded the amount of time needed to complete the step for all 10 quadrats and then divided the total time by 10 to get the average amount of time per quadrat. Once the scanned data were accessed through ArcCatalog, we pulled the raster image of the paper data sheet into ArcMap. We created point and polygon shapefiles for each quadrat and modified their attribute tables using the VBA/Macros function in ArcMap. We used the construction tools in the editor function to digitize the perennial graminoid and several forb species as polygon features and the remaining forb species as point features. Using the “new displacement link” tool in the editor of ArcMap, we spatially adjusted all features to the reference boundary. We calculated the field geometry and saved these edits to complete the data entry process.

For the electronic data capture method, for steps that would typically be completed for several quadrats at one time (i.e., transferring files from laptop to office computer and creating a folder connection in ArcCatalog), we recorded the amount of time needed to complete the step for all 10 quadrats and then divided the total time by 10 to get the average amount of time per quadrat. Once we accessed the files through ArcCatalog, we pulled the edited point and polygon shapefiles and the Plot-Specific Grid Template for each plot in to ArcMap. Using the “new displacement link” tool in the editor of ArcMap, we spatially adjusted all features to a reference boundary. We calculated the field geometry and saved these edits to complete the data entry process for the electronic data capture method.

Statistical Analysis

We obtained sums, means, and standard deviations for the field, office, and total time for the traditional paper-based and electronic data capture methods. Since the data used in this analysis were the times recorded for each step of each method, and each method varied in the number of steps required for the “field”, “office”, and “total”, then there was an unequal number of observations and an unequal variance between the sample sizes used for each method. To account for this difference in sample size and variance, we compared means and standard deviations between methods using a two-sample unequal variance heteroscedastic Student’s T-test (Ott and Longnecker 2008). We tested for linear correlation between percent cover and the amount of time required to map each quadrat using a Pearson correlation coefficient (Ott and Longnecker 2008).

Results

All units from the following analyses are reported in time (h:mm:ss). Means, standard deviations, and p-values are reported in Figure 3.4 and Table 3.1. The average total time (n=10) for the traditional paper-based method was 1:33:37 with a standard deviation of 0:41:53, while the electronic field data capture method was 1:06:48 with a standard deviation of 0:24:09. The average field time for the traditional paper-based method was 0:39:39 with a standard deviation of 0:14:12, while the electronic field data capture method was nearly doubled at 1:03:20 with a standard deviation of 0:23:31. The average office time for the traditional paper-based method was 0:53:58 with a standard deviation of 0:27:40,

while the electronic field data capture method was reduced to 0:03:27 with a standard deviation of 0:00:38.

Of the 10 quadrats sampled, one quadrat (Q91) was nearly devoid of vegetation ($>0.5\%$ cover), while the other quadrats contained between 8-30% cover. We found a correlation between the percent cover and amount of time required to map each quadrat for both the traditional paper-based method and the electronic field capture method. The Pearson correlation coefficient was 0.935 and 0.895 for the traditional paper-based and electronic field capture methods, respectively.

This large difference in herbaceous cover values led to a large standard deviation for the average field time for both methods; however, since the electronic field capture method requires more field time this translated into a proportionately larger standard deviation. Further analysis concluded that Q91 was not a significant outlier (Grubbs' test; Grubbs 1950, Ott and Longnecker 2008). However, since our purpose was to determine how long it took to map quadrats with vegetation, we conducted the analysis again without Q91 to see whether or not this relatively bare plot had a significant influence on the p-values for the average field, office, and total times. The overall trend did not change when Q91 was excluded (i.e., field time increased, office time diminished, total time decreased for the electronic data capture method), however, excluding Q91 did alter the p-values, resulting in a higher level of significance in these findings (Table 3.1 and Figure 3.5).

Discussion and Conclusions

Our results suggest that there are qualitative trade-offs that exist between the traditional paper-based and electronic field data capture methods. The electronic field data capture method increases field time and accuracy while it diminishes the office time significantly and eliminates the transcription process by allowing the user to digitize each quadrat in the field. These crucial differences result in an overall decrease in total time per quadrat for the electronic field data capture method.

For quadrats that are bare or nearly bare, there is no difference in efficiency between methods, as revealed by Q91. The absence, or near absence, of individual plants to map allows for the rapid digitizing of these quadrats regardless of which method is employed. For quadrats that are not bare and have plants to map, the electronic field data capture method decreases the overall amount of time per quadrat on average by almost 0.5 hours, for an average decrease of approximately 44 hours per field season for the 98 chart quadrats used in the larger study (see Chapter 2 of this thesis). Decreasing the amount of money and time spent on data collection and entry allows researchers to allocate those funds elsewhere in the project budget.

Considering the amount of money and time invested in data collection and entry, and how data quality can affect the analysis and conclusions of a study, it is worthwhile to explore options that may increase efficiency and accuracy (Inman-Narahari et al. 2010). Limited funding available for field data collection and

entry has created an urgent need to develop new GIS applications that will decrease the amount of time and labor necessary to complete field data collection.

Developing new methods of digitizing data in the field will improve quality assurance and quality control from the inception of data collection while decreasing the amount of time and labor needed to complete annual field data collection (Buller 2004). By quantifying this increase in efficiency and data accuracy, we aim to provide evidence that digital collection methods for mapping chart quadrats in fine-scale permanent plots can improve herbaceous vegetation monitoring and long-term ecological studies.

Electronic data collection has been proven to enhance ecological research capacity, yet researchers remain reluctant to adopt digital methods for the following reasons: concern of losing large amounts of data, initial investment required to purchase and implement new system, the weather-resistance of electronic devices, and lack of familiarity with digital options (Inman-Narahari et al. 2010). Past attempts to develop electronic field capture methods have been developed; however, technological and computational limitations impeded the widespread use of these methods (Mack and Pyke 1979, Roskier et al. 1997).

While these concerns do hold merit, digital technology has improved greatly in recent years to become more secure, rugged, economical, and user friendly (Inman-Narahari et al. 2010). The field computers used in this study are completely water-resistant and shock-resistant, with data entry by keyboard or touchscreen, and digitizing by mouse or stylus (digital pen). The stylus allows the user to draw polygons or polylines into ArcMap as they would on a traditional

paper datasheet, thus increasing the usability of the digital method (Clegg et al. 2006). Finally, implementing protocols described in this study that require frequent saving on both laptop and portable USB drive reduces the risk of losing large amounts of data.

Recent studies have quantified the increase in efficiency resulting from the use of digital collection methods for mapping and measuring trees in large-scale permanent forest dynamic plots (Inman-Narahari et al. 2010). With this case study, we have quantified a similar increase in efficiency resulting from the use of digital collection methods for mapping the vegetation in fine-scale 1-m² permanent chart quadrats. Case studies such as these document the increase in efficiency that results from the use of digital data collection methods, which is applicable to any ecological study that requires the mapping of vegetation based spatial location within a circumscribed area through the use of a grid system, regardless of the scale of plot.

The key here is to spatially adjust the grid to a reference boundary that can translate easily to units of measure applicable to the specific study (i.e., 1-m² quadrats, this study, or 20-m² quadrats for the Inman-Narahari et al. 2010 study).

The drawback to electronic data collection is the initial investment of the field computer with enough processing power to run ArcGIS 10.2.2 and memory to back-up all field files. Initially, we designed this study to collect these data using ArcPad on a tablet. However, we found that the lower processing power built into most tablets limited the performance of ArcPad in practice causing the application to be highly unstable. As technology advances, tablets will likely be

designed with higher levels of processing power, enabling the electronic field data capture method to run smoothly both in ArcMap and ArcPad.

Employing the electronic field data capture method to digitize herbaceous vegetation on permanent chart quadrats will increase the time spent in the field; however, this approach will almost eliminate the time needed to enter data back in the office. Transitioning to the electronic field data capture method of mapping chart quadrats will decrease the amount labor needed to collect and digitize data, reduce the likelihood that transposition or scientific errors will occur during data collection, and increase our ability to search and manipulate the field data (Buller 2004). By implementing the electronic field data capture method of mapping chart quadrats, we can streamline the field data collection, while improving quality assurance and quality control.

Table 3.1. Average field, office, and total time for each method and corresponding p-values derived from the two sample unequal variance heteroscedastic Student T test. Times are reported in hours:minutes:seconds (h:mm:ss).

	Traditional Method	Electronic Method	P-Values
All Quadrats Included			
Field Average	0:39:39	1:03:20	0.102
Office Average	0:53:58	0:03:27	0.005
Total Average	1:33:37	1:06:48	0.671
Q91 Excluded			
Field Average	0:42:34	1:06:56	0.004
Office Average	0:58:29	0:04:51	0.000
Total Average	1:41:03	1:11:48	0.131

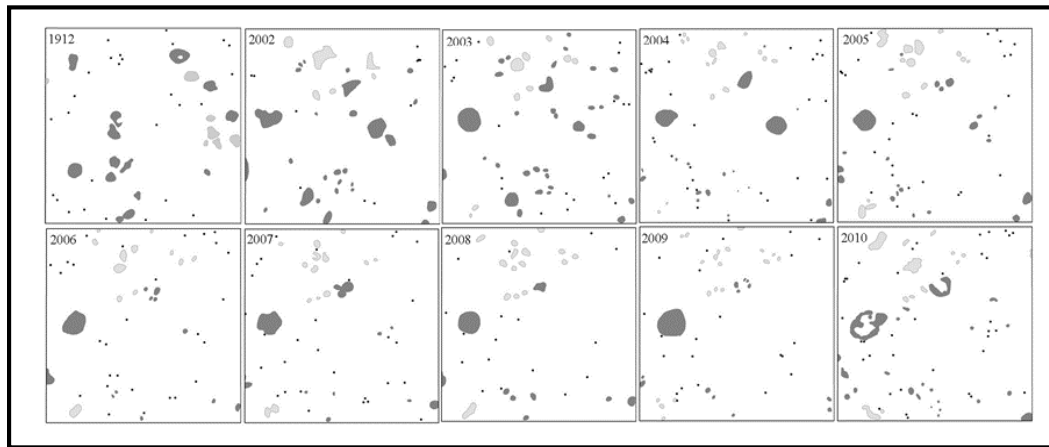


Figure 3.1: Digitized images of herbaceous vegetation on one chart quadrat at the Black Springs site through time. The top left panel illustrates the 1912 plant cover, and the remaining panels are consecutive quadrat maps from 2002 through 2010. Dark grey polygons represent basal cover of C₃ graminoids, light grey polygons represent C₄ graminoids, and points represent annual and forb species at the Black Springs site (R. T. Strahan, unpublished data).

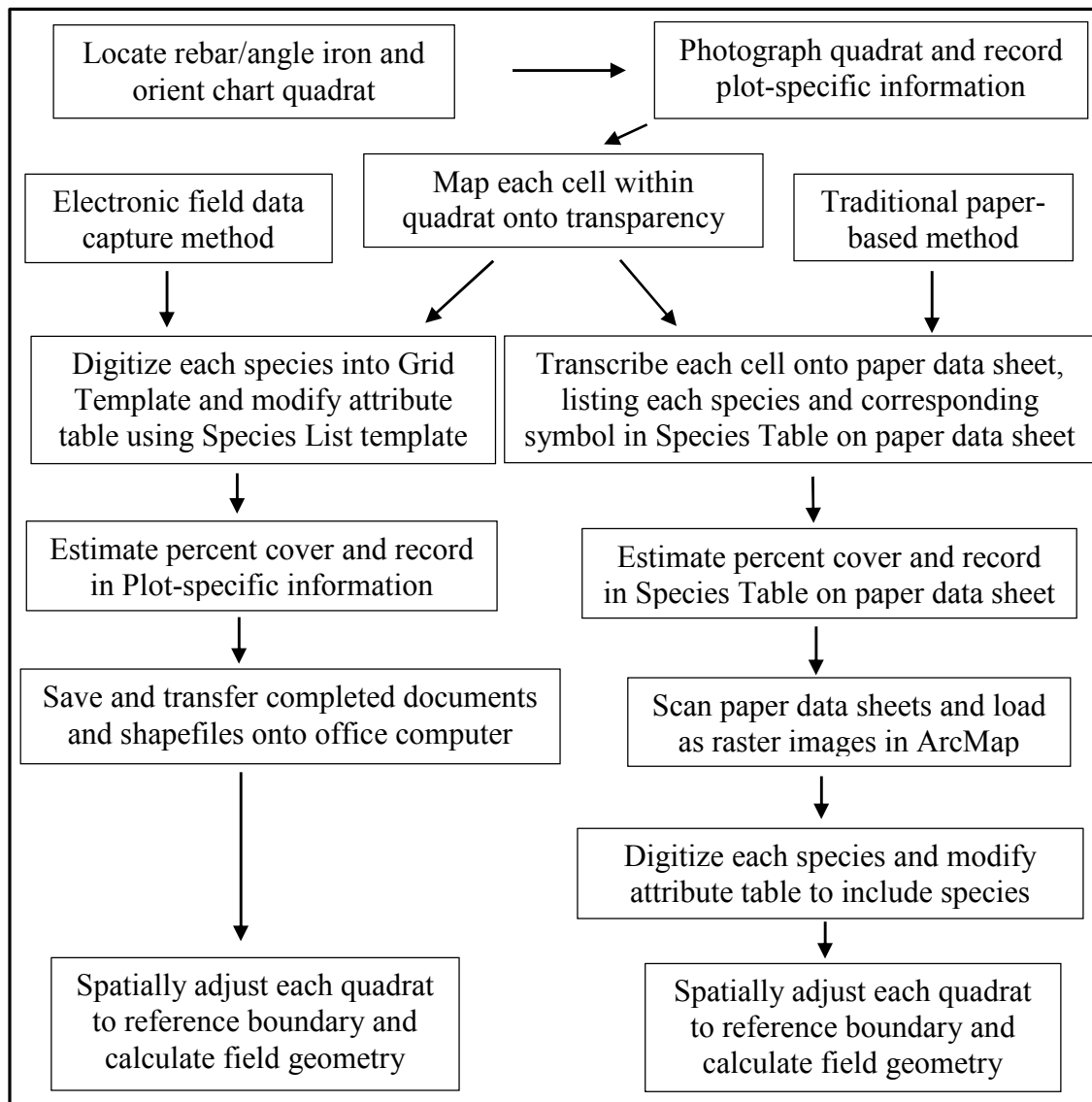


Figure 3.2. Work flow diagram illustrating the similarities and differences between the traditional paper-based method and the electronic field data capture method.

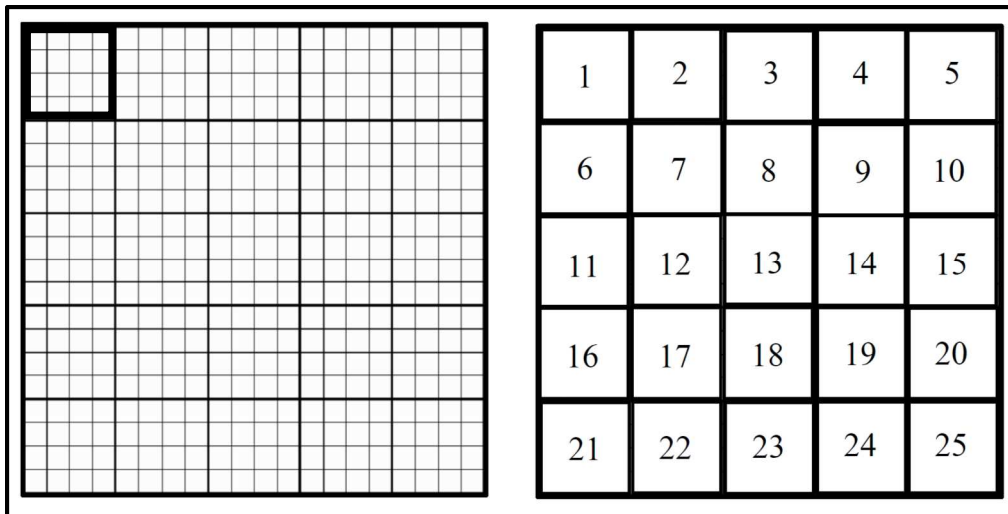


Figure 3.3. The large 1-m² sampling frame (left) is divided into a grid of 25 cells (right), each of which contains a fine-grained grid to facilitate the mapping of individual plants to scale based on their location within the quadrat. The bolded black box in the upper left corner of the sampling frame (left) corresponds to grid cell “one” on the right.

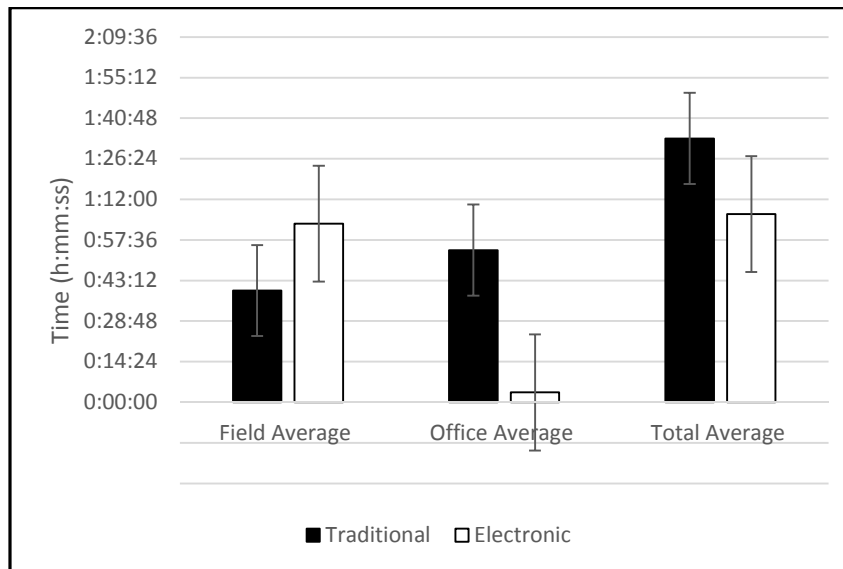


Figure 3.4. Average difference for field, office, and total time between the traditional paper-based and electronic field data capture methods with error bars indicating standard deviation (all quadrats included).

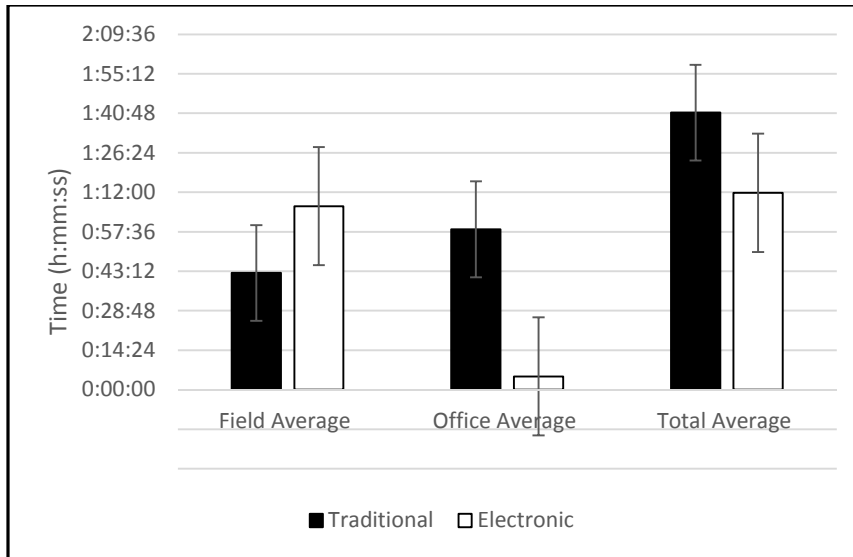


Figure 3.5. Average difference for field, office, and total time between the traditional paper-based and electronic field data capture methods with error bars indicating standard deviation (Q91 excluded).

CHAPTER 4:
DIRECT EFFECTS OF SEASONAL PRECIPITATION ON THE
DEMOGRAPHY OF ARIZONA FESCUE

Abstract

We used detailed local climate variables and data from an annually remapped dataset (2002-2014) described in Chapter 2 to examine the effects of seasonal precipitation on the key demographic rates of Arizona fescue (*Festuca arizonica* Vasey). We reconstructed life tables to examine the vital rates (e.g., survival probabilities, growth, and life expectancies) of Arizona fescue. We made population projections using the species' state (size) and precipitation variables using Integral Projection Models (IPMs) to quantify the direct influence of seasonal precipitation on the vital rates of this species. We pooled the demographic data for all 13 years, with the corresponding seasonal precipitation covariates from that year, into one data frame to estimate the survival/growth kernel of the IPM. We confirmed the notion that growth was dependent upon spring precipitation and survival was dependent upon winter precipitation for Arizona fescue. We estimated the population growth rate and predicted a stable size distribution from the discretized survival/growth kernel. Incorporating information derived from data-driven models into adaptive management strategies enables land managers to predict shifts in plant populations and community composition, forage production, and ecosystem function.

Key words: plant populations, long-term datasets, perennial graminoid, Integral Projection Models, *Festuca arizonica*, Southwest

Introduction

In an era characterized by anthropogenic climate and land-use change, understanding the impact of these changes on plant populations and community dynamics has taken on a new level of urgency (Dalglish et al. 2010, Adler et al. 2012, Chu et al. 2013). Our ability to predict vegetation dynamics is restricted by our current lack of understanding of how plant populations are influenced by climate change because climatic variation is the primary driver of interannual variation in population growth rates in many ecosystems (Laurenroth and Adler 2008, Dalglish et al. 2011, Adler et al. 2012, Adler et al. 2013, Chu et al. 2014).

Current theoretical and empirical evidence suggests that climate variation may increase the variability of demographic rates for many species, potentially altering demographics at the community level (Dalglish et al. 2010). One valuable approach to predicting population responses to climate change is to describe the relationships between climate variables and demographic rates that emerge from the synthesis of long-term observational data (Adler et al. 2013). We used detailed local climate variables and a dataset from the annually remapped (2002-2014) chart quadrats described in Chapter 2 to examine the effects of climate on the demographic rates of a dominant, cool-season, bunchgrass species, Arizona fescue (*Festuca arizonica* Vasey).

In the semi-arid ecosystems of the Southwest, the cover of perennial bunchgrasses can vary greatly from year to year, challenging land managers to adopt new strategies for gauging forage production (Dalglish et al. 2011). Since Euro-American settlement, fire suppression and livestock grazing practices have

induced a significant shift in the structure of southwestern ponderosa pine dominated forests, profoundly impacting the herbaceous understory in these frequent-fire ecosystems (Covington and Moore 1994*a* and *b*). For these perennial bunchgrass species, the importance of growth, survival and recruitment varies significantly with genet size, which exhibits a great amount of interannual variation (Laurenroth and Adler 2008, Dalgleish et al. 2011, Chu et al. 2014).

The factors that affect genet size have the potential of creating feedbacks between the size distribution of genets, the population growth rates, and the availability of forage (Dalgleish et al 2011). Altered population growth of a dominant species could have profound effects on community structure and ecosystem function (Dalgleish et al. 2011). Therefore, the size structure of dominant bunchgrass populations can be altered greatly by changes in climate or land-use practices, potentially altering plant population structure, community dynamics, and ecosystem function.

To examine the size structure of this Arizona fescue population, we first reconstructed life tables to examine vital rates (e.g., survival probabilities, growth, and life expectancies) from long-term observational data derived from the core data set described in Chapter 2. We then made population projections using the species' state (size) and precipitation variables using Integral Projection Models (IPMs) to quantify the direct influence of seasonal precipitation on the vital rates of this perennial bunchgrass.

We predicted that survival and growth for this cool-season (C_3 photosynthetic pathway) perennial bunchgrass to be dependent upon winter and

spring precipitation based on previous descriptions of the phenology for Arizona fescue (Pearson 1942, Pearson 1967, Clary 1975). Incorporating information derived from data-driven models into adaptive management strategies enables land managers to predict shifts in plant populations and community composition, forage production, and ecosystem function. Through science-based approaches to predicting shifts in plant populations, which are the result of anthropogenic climate and land-use change, we can attempt to mitigate the impacts of climate change and adapt our land-use practices to restore and conserve native plant populations and communities. Gaining a better understanding of the climatic factors that drive plant population demography will allow land managers to make informed decisions regarding land-use practices and the implementation of restoration treatments in the Southwest.

Methods

Study Area and Data Description

The demographic data used in this study were derived from a set of 98 permanent chart quadrats established between 1912 and 1927 to examine: 1) the effects of grazing on the herbaceous plant community, 2) grass competition with pine seedling establishment, and 3) initial patterns of plant succession (see Chapter 2, this thesis, Talbot and Hill 1923, Pearson 1923, 1933, 1942; Arnold 1950). Spanning the elevational range of ponderosa pine (2,000-2,500 m), all quadrats are found on soil types derived from basalt, limestone, and sandstone parent materials and are located within 40 km of Flagstaff, Arizona on the Coconino National Forest and the Fort Valley Experimental Forest.

Ponderosa pine (*Pinus ponderosa* Laws. var. *scopularum* Englem.) and Gambel oak (*Quercus gambelii* Nutt. Var. *bonina* S.L. Welsh) dominate the overstory vegetation, while greater diversity exists in the understory shrub and herbaceous plant communities. Arizona fescue is the focal species in this study, which is a widely abundant perennial, cool-season (C₃ photosynthetic pathway), bunchgrass species that is present throughout our study area. Refer to Chapter 2 for a detailed description and history of the study area and data.

We used detailed climate records to calculate mean monthly precipitation and temperature from the nearby Pullman Airport weather station where daily and monthly observations are recorded. The mean annual precipitation from 2002-2013 was 491 mm and the mean annual temperature was 6.6° C, typical of the semi-arid ecosystems of the Southwest.

Extracting Demographic Data

Demographic information is rare for herbaceous plants, however, the fine-scale spatial resolution of chart quadrat maps enables us to track the fate of each individual plant over time and analyze spatial patterns over time (Clements 1905, Laurenroth and Adler 2008, Zachmann 2010). Original chart quadrat maps were digitized and spatially referenced in a geographic information system (ArcGIS 10.2.2) allowing for the calculation of demographic parameters (survivorship and life expectancy at age 1) (Laurenroth and Adler 2008, Strahan 2013).

Survivorship (year 1 survival) is an estimate of the probability of an individual surviving from year 1 to year 2 (Laurenroth and Adler 2008). Life expectancy is

a measure of the average number of years an individual is expected to live once it has reached age 1 (Laurenroth and Adler 2008, Strahan 2013).

We determined demographic parameters for Arizona fescue using computer programs developed by Dr. Peter B. Adler (Utah State University) that build life tables through the use of two basic rules that classify genets based on their spatial location within the quadrat (Fair et al. 1999, Laurenroth and Adler 2008). These scripts determine whether an individual is deemed a survivor or a new recruit based on its spatial location in reference to conspecific individuals within the quadrat by applying a 5 cm buffer designed to account for both mapper error and the potential for vegetative growth (Fair et al. 1999, Laurenroth and Adler 2008).

Perennial grass species are mapped as polygon features wherein the tracking rules are based on areas of overlapping polygons. At time $t - 1$, a 5 cm buffer is added to all polygons of a given species. If an individual overlaps with any conspecific polygon in year t it is given the identity of the individual with which it shares the greatest overlap, otherwise it is labeled a new recruit (Laurenroth and Adler 2008). This perennial graminoid is known to exhibit clonal growth, and these assumptions and tracking rules are designed to account for the coalescing and fragmenting of individual plants over time.

Incorporating Climate Variables

Using detailed climate records from the nearby Pullman Airport weather station, we obtained mean monthly precipitation from 2002-2013. To represent seasonal precipitation, we binned the climate data into three distinct periods of the

year that represent winter, spring, and summer monsoonal precipitation northern Arizona (Table 4.1). The mean monthly precipitation was averaged over the corresponding months to obtain a mean seasonal precipitation value for each covariate. The covariates were inputted into the data frame for size at t and size at $t + 1$ using the covariate and covariateNext function of *IPMpack* (Metcalf et al. 2013). We followed the same assumptions as Dalglish and others (2011) which assume that kernels and climate variables at time $t + 1$ are independent of time t , consistent with the absence of autocorrelation in the climate record.

Stage-Based Models

Stage-based models are based on the theory that organisms move through life in a pattern of distinct stages over time and that these stages can be described based on their distinguishing characteristics (Caswell 2001, Silvertown and Charlesworth 2001). If the vital rates of a population depend on size and if growth is sufficiently plastic, then the demography of the population is dependent on size more than the developmental stage because it is possible for individuals within the multi-stage process to revert to earlier stages or skip some stages entirely (Caswell 2001). This is the case for perennial graminoids, because the size of an individual can change drastically at any stage of life (Silvertown and Charlesworth 2001). For size-structured populations such as these, that exhibit size-dependent demography, stage must be represented as a continuous variable (Caswell 2001).

Integral projection models (IPMs) are commonly used to examine the how changes in individual animal or plant performance influence population dynamics

for continuously structured populations where some continuous measure of individual state (i.e., size) influences growth, survival, or reproduction (Rees et al. 2014). Since size and growth of Arizona fescue is known to rapidly change at any stage of life, we suspect this to be a size-structured population. Therefore, an Integral Projection Model is the best tool to examine population dynamics because it is designed to incorporate the individual's state as a continuous stage variable (Metcalf et al. 2013, Merow et al. 2014, Rees et al. 2014).

Constructing Integral Projection Models

Differentiated from matrix projection models, which project discrete population structure in discrete time, IPMs are constructed from regression models predicting vital rates from continuous state variables (e.g., size or age) and covariates (e.g., climate, soils, etc.) that provide mechanistic insight into emergent ecological patterns (Merow et al. 2014). Here we used *IPMpack*, an R package designed to incorporate a wide variety of life histories, including both continuous and discrete life stages, as well as dependence in vital rates on covariates (Metcalf et al. 2013).

For populations structured by a single continuous variable such as size, the state of the population is described by the probability density function $n(x, t)$. This defines the proportion of individuals of size x at time t . the integral projection model for the number of individual's size y at time $t + 1$ is given by

$$n(y, t + 1) = \int_L^U K(y, x)n(x, t)dx$$

where the kernel $K(y,x)$ represented a matrix of all possible transitions from size x to size y . The integration is carried out over all possible sizes bound by L and U , the respective lower and upper limits (Metcalf et al. 2013).

The kernel K can be broken down into two vital rate functions, $P(y,x)$ and $F(y,x)$, where $P(y,x)$ represents a matrix of transitions attributable to survival and growth (i.e., a survival/growth kernel or P matrix) transitions, and the $F(y,x)$ describes per-capita contributions of reproductive individuals (Metcalf et al. 2013). We did not have fecundity data (e.g., seed stalks, flowering, seeds, etc.) for Arizona fescue, therefore our dataset does not include data pertaining to fecundity or sexual reproduction (i.e., F matrix). Furthermore, in order to conduct sensitivity and elasticity analyses, both the P matrix and the F matrix must be incorporated into the K kernel, so we could not provide sensitivity or elasticity analyses.

We use the probability densities of growth between continuous stages (i.e., size) conditional on survival in combination with climate variables modeled in discrete time steps to construct a survival/growth kernel (P matrix) that allows us to examine the direct effect of seasonal precipitation on growth and survival (Merow et al. 2014).

We formatted the data according to the requirements of *IPMpack*, and entered as a data-frame object (a table of rows and columns) (Table 4.2), wherein each row represents an individual at time t and time $t + 1$. We pooled the demographic data for all 13 years, with the corresponding covariates from that year, into one data frame to estimate the survival/growth kernel of the IPM

(Easterling 2000). This allowed us to examine the effect of precipitation on the growth and survival for this dominant graminoid from 2002-2013, however, it should be noted that the sample size reported in the IPM section of the results is inflated because each individual is counted as one sample for each year that it was censured. The true population size is listed in the life tables found in Table 4.4, which display the demographic data from 2002-2014 derived from the scripts (Laurenroth and Adler 2008).

Statistical Analysis

To quantify the relationships that survival and size at time $t + 1$ have with size, we build survival and growth objects using the *IPMpack* functions *makeSurvObj* and *makeGrowthObj* which specify the desired combination of covariates related to size used in predicting vital rates. For survival and growth objects, appropriate methods are defined that implement the model by applying the midpoint rule to obtain the P component of the IPM (i.e., $Pmatrix$) using a range of mesh sizes (i.e., the division of size range into artificial size classes of equal width) to ensure accurate estimates of population dynamics (Ellner and Rees 2006, Dalgleish et al. 2011, Metcalf et al. 2013, Rees et al. 2014). Once the $Pmatrix$ was obtained, we checked the validity of the final IPM using the *diagnosticsPmatrix* function in *IPMpack*.

The advantage of *IPMpack* is that this R package contains a huge array of statistical models reflecting the diversity of functional forms as well as error structures and transforms of response variables written in object-oriented code (Metcalf et al. 2013). Survival and growth classes are defined within *IPMpack*

using features of R that contain linear models relating transforms of size and covariates to the vital rate of interest. The model selection process follows the same general approach to selecting functional forms for components of a kernel for any IPM as outlined by Easterling (2000). In this general approach, the fitted linear model was tested against nonlinear alternatives and the significance of nonlinear terms was tested using the ANOVA function with X^2 test statistic (Clark et al. 1992).

The survival and growth function $p(x,y)$ was divided into two separate survival and growth components in the following equation:

$$p(x,y) = s(x)g(x,y)$$

where $s(x)$ is the survival probability of a size- x individual, and $g(x,y)$ is the probability of a size- x individual growing to be size y (Ferrer-Caevantes et al. 2012). The survival probability $s(x)$ was modeled as a logistic regression:

$$\text{logit}[s(x,\theta)] = \beta_0 + \beta_s x + \beta_{c,1}\theta_1 + \dots + \beta_{c,i}\theta_i + \varepsilon$$

where x is the log of genet basal area, β_0 is an intercept parameter β_s is a slope parameter for size, θ is a vector of climate variables for i number of variables, $\beta_{c,i}$ is a slope parameter for the j th effect of climate, and ε is the error term (Dalglish et al. 2011). Genet growth $g(x,y)$ was estimated through linear regression:

$$\mu_g(x,\theta) = \beta_0 + \beta_s x + \beta_{c,1}\theta_1 + \dots + \beta_{c,i}\theta_i + \varepsilon$$

where $\mu_g(x,\theta)$ is the predicted size at time $t + 1$, and β_0 , β_s , θ , $\beta_{c,j}$, and ε are as described above (Dalglish et al. 2011, Ferrer-Caervantes et al. 2012). Summaries of the AIC and p-values for each model compared for Arizona fescue can be found in Table 4.3 in the Appendix.

To construct the survival/growth kernel K from the P matrix, survival and growth functions underlying the P matrix are obtained from statistical models of the data. A key element of construction of an IPM is appropriate statistical model selection and expression of conditionalities in the vital rate models that underlie the IPM and are obtained by regressing survival and growth on the relevant state variable (i.e., size at time t) (Metcalf et al. 2013). *IPMpack* has a range of model comparison functions that can fit any number of models for survival and growth functions and plot the results on a single figure (Metcalf et al. 2013).

The ‘pair-wise’ model selection process is a reiterative process testing multiple models, all of which test the significance of the continuous variable size and precipitation covariates on survival and growth. Once determined, the ‘best fit’ model (i.e., lowest AIC) for survival and growth is then implemented by applying the midpoint rule for numerical integration to obtain a high-dimensional matrix (Metcalf et al. 2013). The continuous projection kernel is a nonnegative surface representing all possible transitions from size x to size y , where the population size distribution is described by a density function, and the vital rates are a function of genet size (x) and vector of time-varying climate variables (Easterling 2000, Dalglish et al. 2011, Dahlgren and Ehrlén 2011).

The population growth rate (λ) is a ratio of N_t/N_{t-1} that provides an estimate for the population’s change or flux over time (Gibson 2002). This ratio indicates a population that is increasing in time when $\lambda > 1$, a population in decline when $\lambda < 1$, and a population that is unchanging or in stasis when $\lambda = 1$ (Gibson 2002). The stable population growth theory describes the existence of a

unique stable population distribution that a density-independent population will converge on from an initial composition, which is referred to as the ‘stable size distribution’ (Ellner and Rees 2006, Rees et al. 2014). The ‘stable size distribution’ and population growth rate (λ) are estimated directly from the discretized survival/growth kernel.

Results

Demographic Analyses – Life Table

From 2002-2014, 228 individuals were included in the census data for Arizona fescue (Table 4.4). During that period, the first year survival for Arizona fescue was 0.491, meaning that approximately half of 1-year-old individuals survived to year 2. The life expectancy for Arizona fescue during that period was 2.847, meaning that the number of years an individual is expected to live past 1 year old was approximately 2.8 years. The peak expectancy, which is the longest life expectancy associated with a given age, was 4.3 years and the age at peak was 2 years old. Maximum life span was 13 years indicating that some individuals in the population were present in 2002 and survived through 2014. It should be noted that maximum life span is representative of the length of the dataset and does not accurately represent the *potential* maximum life span for this species.

Life expectancy nearly doubles between age 1 and age 2, and first year survival suggests that approximately half of the individuals that survive to reach age 1 will survive to reach age 2, which is the age class associated with the “longest” life expectancy for this population. Figure 4.1 illustrates the life cycle of a perennial bunchgrass, the annual census period occurs in the month of August

which corresponds with the vegetative growth period for plants utilizing a C₃ photosynthetic pathway such as Arizona fescue. Vegetative growth is measured for perennial plants by mapping and digitizing of the basal area of the plant, which is then inputted into the data frame as size at time t and $t + 1$.

IPM Analyses

Year-to-year changes in size along with the linear regression fit for mean size in year $t + 1$ are found in Fig.4.3 along with survival and growth (Easterling 2000). Since the linear relationship between the size at time t and the size at time $t + 1$ with mean growth in genet basal area from t to $t + 1$ is described as a linear function, then the use of size in modelling the population dynamics for Arizona fescue is tenable because this indicates a population structured by size (Caswell 2001, Silvertown and Charlesworth 2001, Dalgleish et al 2011, Ferrer-Caevantes 2012). The annual survival probability increases exponentially until genet size in time t is approximately 100 cm² (Fig.4.3), where the probability of survival levels off with a 0.95 chance of survival (Rees et al. 2014).

The size distribution and age-specific trajectory for survival (Fig.4.2 and Fig.4.4, respectively) indicate that this species follows a Type III survivorship curve that is produced when the age-specific mortality rate decreases with increasing t (Pinder et al. 1978). This finding is consistent with the survival curves (Fig.4.3) because genet size has the highest influence on the individuals probability of survival, and generally the genets in the largest size classes are also the longest lived, therefore the probability of survival increases with size which increases with age. Comparing the current size distribution (Fig.4.2) with the

survival probability for this population (Fig. 4.3) reveals that the majority of individuals in this population belong to the smallest size classes (less than 10 cm²) which corresponds with an annual survival probability of approximately 0.65. Few individuals in the population have survived and transitioned into size classes greater than 100 cm², corresponding with survival probability of approximately 0.95, which is also consistent with a Type III survivorship curve (Pinder et al. 1978).

Figure 4.5 contains the diagnostic plots for the fitted survival and growth objects (derived from the *makeSurvObj* and *makeGrowthObj* functions) including size range, survival, and life expectancy, which were obtained from the *diagnosticsPmatrix* function of *IPMpack*. Since the three lines fall along the (0, 1) line shown in grey on the middle panel (i.e., survival) of Fig. 4.5, this indicates that the appropriate minimum and maximum bin size have been applied to the *Pmatrix* (Metcalf et al. 2014).

The reiterative model selection process revealed that survival and growth are both a function of size. When precipitation variables were added to linear models including size, we were able to determine which precipitation covariates had the greatest influence on the survival and growth of Arizona fescue (Table 4.3 in the Appendix). The ‘best fit’ model for survival included a quadratic term for winter precipitation as follows: logsize + winter precipitation + winter precipitation². The ‘best fit’ model for growth of Arizona fescue included spring precipitation and is as follows: logsize + spring precipitation. Once the

‘best fit’ models were identified, the ‘best fit’ models were incorporated into the survival and growth functions of the IPM.

The fitted survival function (Fig. 4.6) indicates the probability of an individual surviving from t to $t + 1$ is strongly associated with winter precipitation. The fitted growth function (Fig. 4.6) indicates that growth of Arizona fescue is strongly associated with spring precipitation. The ‘best fit’ models for survival and growth included parameters that incorporate these relationships into the survival and growth functions in the final IPM for Arizona fescue.

The stable size distribution shows the proportion of size classes in the population when it has reached a constant population growth rate (λ) and it is skewed towards individuals in the intermediate to large size class range (Fig. 4.7). Population rate of increase (λ) is estimated from the final survival/growth kernel for this Arizona fescue population and is 0.869. Since we pooled demographic data from 2002-2013, this can be thought of as the average population growth rate for Arizona fescue from 2002-2013. We had expected a population growth rate that was in decline (i.e., $\lambda < 1$) due to the dramatic shift in forest structure that has occurred throughout our study area in the past century. Low population growth rates (λ) may arise for a variety of reasons as decreases in vital rates can be due to both fine-scale factors (i.e., soils, site quality, neighborhood competition) and coarse-scale factors (i.e., climate and land-use practices) (Jongejans et al. 2010a). Since Arizona fescue is widely abundant throughout our study area, we suspect two aspects of this dataset that may be affecting the accuracy of this population growth rate estimate are: (1) there was a severe drought in 2002 at the beginning

of the study period which may have lowered the average population growth rate from 2002-2013; and (2) the absence of fecundity or reproductive data (F matrix) may lead to lower estimates of the population growth rate because we are only capturing the clonal growth and not the reproductive growth of this population. We would require data pertaining to the population's fecundity prior to concluding that this population is in decline.

The survival/growth kernel describes how individuals survive and change in state (e.g., grow, shrink, or remain the same) through the summation of all investigated parameters for Arizona fescue (survival, growth, and seasonal precipitation) for each individual (Ferrer-Cervantes et al. 2012, Ghosh et al. 2012, Merow et al. 2014). We combined the survival and growth vital rate functions to create the survival/growth kernel, the resulting survival/growth kernel for Arizona fescue can be found in Fig 4.7. The contour lines corresponding to the largest regions of the kernel, containing the highest density of individuals, correspond with the smallest size classes which is consistent with the current size distribution of this population (Silverman 1986, Filippone and Sanguinetti 2011). Similar to a matrix for a size-structured population, the kernel shows the smallest values in the largest contour interval, representing the highest density of individuals in the smallest size class, with the values increasing along the diagonal surface representing survival with the possible transition to a neighboring size class (Lefkovitch 1965, Ferrer-Caervantes et al. 2012).

Discussion

Consistent with previous descriptions of the phenology of Arizona fescue, we found that survival and growth for this C₃ perennial bunchgrass was significantly linked with winter and spring precipitation (Pearson 1942, Pearson 1967, Clary 1975). Our results confirm that the current population size structure of this dominant graminoid is consistent with a Type III survivorship curve descriptive of a population consisting primarily of many small individuals with a low probability of survival and few large individuals with a high probability of survival. Laurenroth and Adler (2008) found that graminoids follow a Type III survivorship curve more strongly than forbs, thus graminoid populations tend to experience the highest rates of mortality in the youngest age classes. Jongejans and others (2010*b*) found that increasing life span led to an increase in population stability and growth rate.

We estimated the current population growth rate to be less than 1 ($\lambda = 0.869$) indicating a population in decline. While this population growth estimate for Arizona fescue may be lower than the true population growth rate, it does provide land manager with a measure of population change over time, which can be used to assess the population in a given year or cumulatively over a period (Gibson 2002). The IPM we have constructed for Arizona fescue provides land managers with a tool to predict how this population may change in response to various climate and land-use scenarios. We conclude that altering the size structure of this perennial bunchgrass population can increase the population growth rate and average life span by increasing the number of individuals

belonging to the larger size classes with higher probabilities of survival. Shifting the size structure of the population to one consistent with the stable size structure can increase the probability of survival for individual genets, thus increasing the life span and growth rate of the population.

Perennial bunchgrass genet size is known to exhibit a significant amount of interannual variation, significantly influencing the population's survival and growth, which can have profound impacts on community composition and ecosystem function (Dalglish et al. 2011). We have identified winter and spring precipitation as climatic factors that have the potential of creating feedbacks between the size distribution of genets, the population growth rates, and the availability of forage (Dalglish et al. 2011).

For populations structured by size, understanding the factors that can alter the size distribution is imperative in developing management strategies that optimize the resource (i.e., forage production, erosion control) and avoid unintentionally altering plant population structure, community dynamics, and ecosystem function. Time series data from size-structured populations, such as data derived from permanent chart quadrats, make it possible to analyze how climatic variability can affect population survival and growth (Albertson and Tomenek 1965, Gibbens et al. 2004, Yao et al. 2006, Laurenroth and Adler 2008, Jongejans et al 2010b, Zachmann 2010).

There are many other biotic and abiotic factors that may influence the survival and growth of Arizona fescue such as: fecundity, competition, tree canopy cover, temperature, elevation, soils, and fuel load. This IPM will allow

for the investigation of other biotic and abiotic factors that may play a role in determining the soil moisture available survival and growth of Arizona fescue.

Alternative grazing practices have been proposed to reduce the negative effects of grazing during drought periods in Arizona (Loeser et al. 2005). Loeser and colleagues demonstrated the importance of climatic variation in determining the ecological effects of grazing practices and recommended implementing adaptive management strategies that anticipate this variation. They concluded that, to improve conservation efforts, grazing intensity should be reduced or eliminated during periods of drought to avoid the effects of overgrazing key forage plants. We conclude that adaptive management strategies can use information derived from IPM's constructed for dominant perennial graminoids to predict how climatic variation may influence the population dynamics of these key forage plants in a given year and adjust land management practices to avoid damaging the resource and initiating an unintended shift from a grassland state to a woodland state (Briske et al. 2008, Loeser et al. 2005).

Understanding the climatic factors that drive plant population demography will allow land managers to make informed decisions regarding land-use practices and the implementation of restoration treatments in the Southwest. As we prepare for a future where climate change will likely cause unprecedented shifts in the distribution of plant populations, focusing restoration efforts on dominant species makes the implementation of landscape-scale restoration initiatives a feasible option because the stability of focal species has implications that span the spectrum of ecosystems from which they persist. Incorporating science-based

approaches into adaptive management strategies enables land managers to predict shifts in plant populations and community composition, forage production, and ecosystem function.

Table 4.1. The months of the year and season represented for each covariate.

Covariates	Months of the year	Season represented
Covariate 1	November-March	Winter Precipitation
Covariate 2	April-June	Spring Precipitation
Covariate 3	July-October	Monsoonal (summer and fall) precipitation

Table 4.2. Description of the variables inputted into the Integral Projection Model data frames for *Arizona fescue*.

Variable	Variable Description
size	Size of individual at time t
sizeNext	Size of individual at time $t + 1$, NA for individuals that are dormant or dead
surv	If the individual was present in $t + 1$, then 1 indicates survival. If the individual did not survive to $t + 1$, then 0 indicated the death of the individual.
stage	Indicates the type of stage that the individual is in at the start of the census interval, since size is best represented as a continuous variable this is continuous for all individuals censored in time t .
stageNext	Continuous unless the individual was dormant in time $t + 1$, which was indicated as “hibernating adult”
covariate1	Value of covariate 1 in time t
covariate2Next	Value of covariate 1 in time $t + 1$
covariate2	Value of covariate 2 in time t
covariate2Next	Value of covariate 2 in time $t + 1$
covariate3	Value of covariate 3 in time t
covariate3Next	Value of covariate 3 in time $t + 1$

Demography

Table 4.4. Life tables for Arizona fescue for demographic data from 2002-2014.

Species	N (Nx)	First Year Survival (lx)	Life Expectancy (Tx)	Peak Expectancy	Age At Peak	Maximum Life Span*
<i>Festuca arizonica</i>	228	0.491	2.847	4.279	2	13

*Maximum life span is equivalent to the number of sampling years (2002-2014).

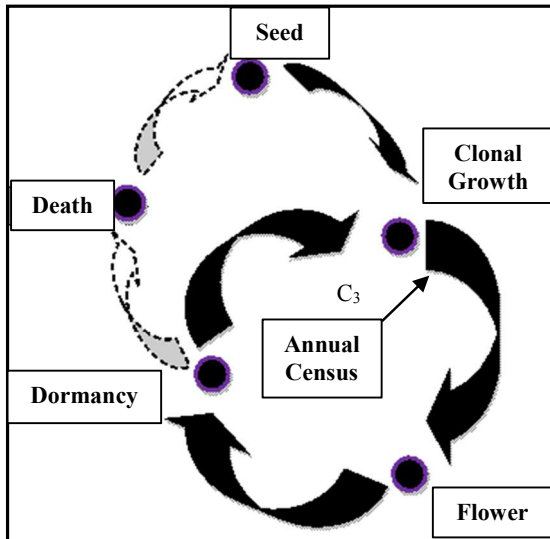


Figure 4.1. Life cycle for perennial bunchgrasses with annual census period indicated for Arizona fescue (C_3) (adapted from <http://bioweb.uwlax.edu>).

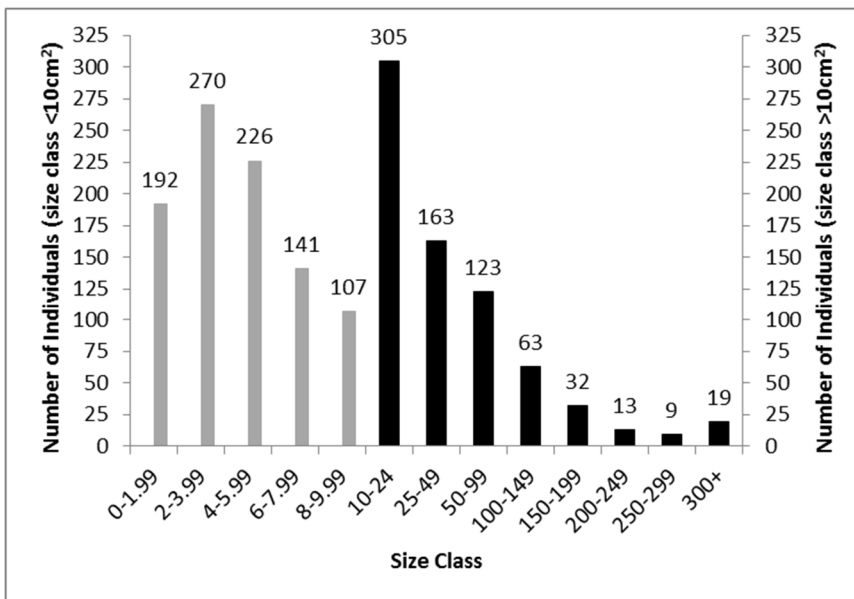


Figure 4.2. Size distribution for Arizona fescue (from 2002-2014).

IPMs

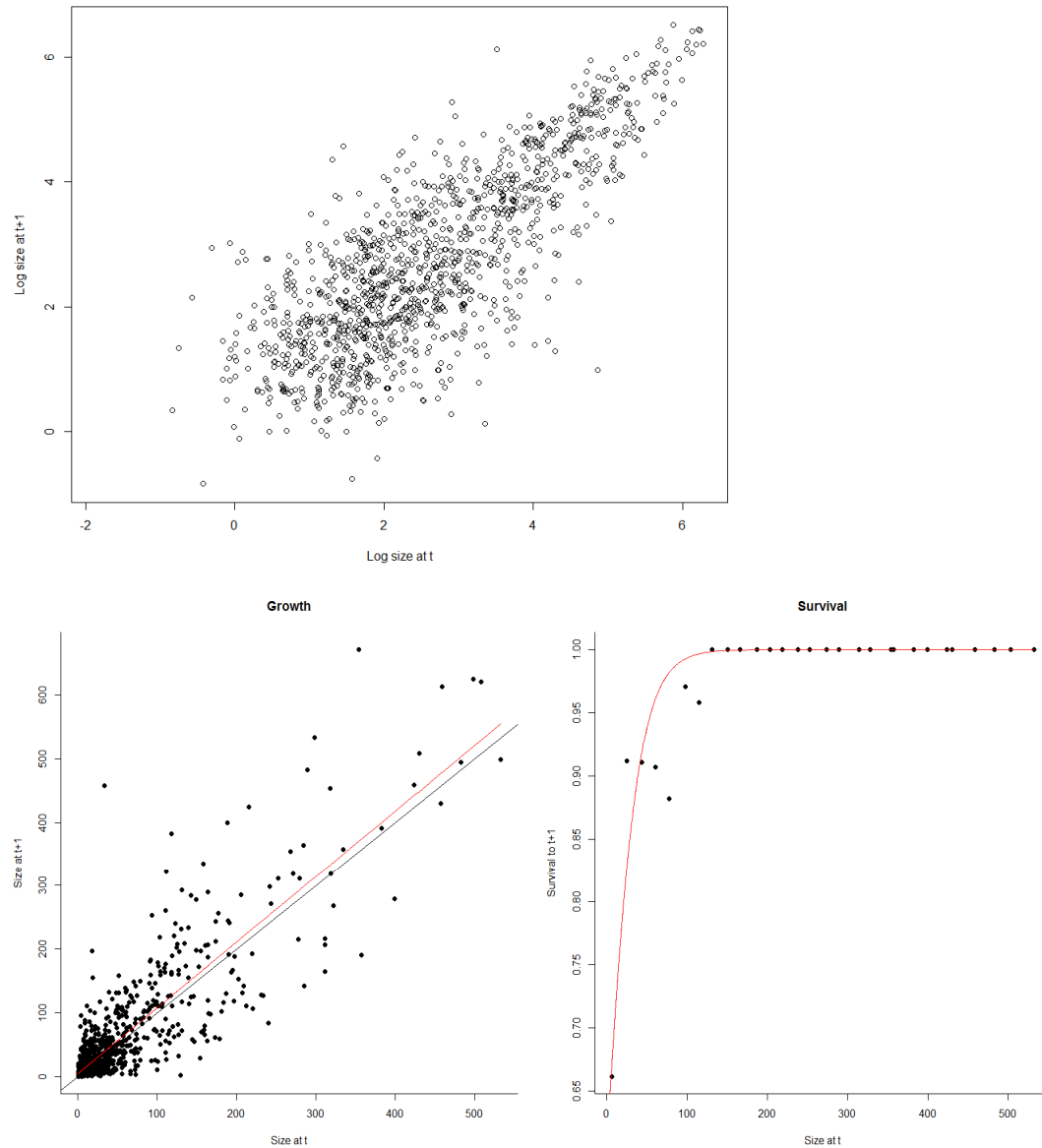


Figure 4.3. Year-to-year changes in size of each individual with the linear regression fit for mean size in year $t + 1$ (top), growth (left) and survival (right) of Arizona fescue from 2002-2013 (size in cm^2).

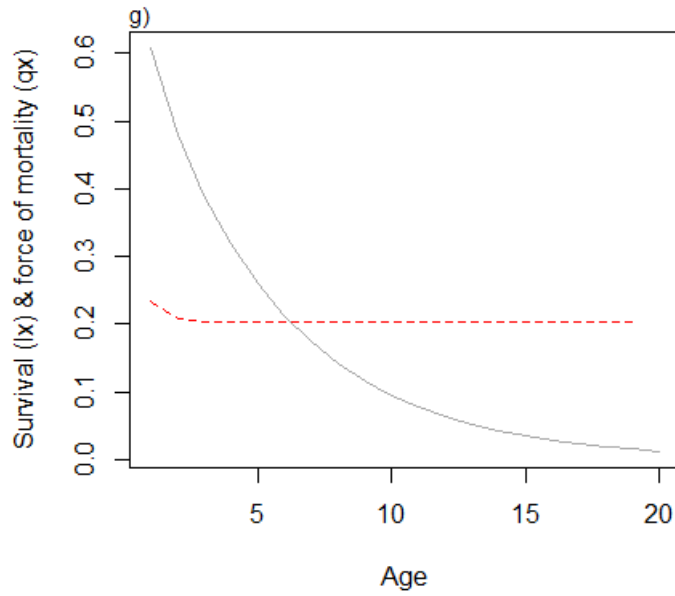


Figure 4.4. Age-specific trajectory for survival (l_x) and force of mortality (q_x) for Arizona fescue.

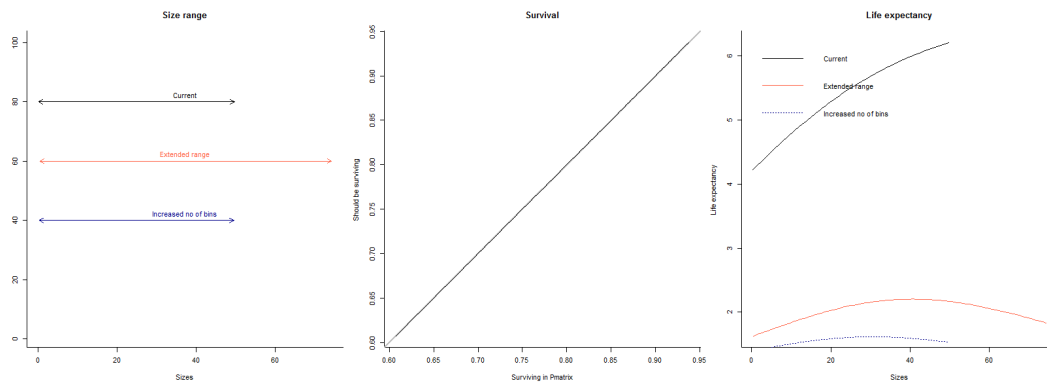


Figure 4.5. Diagnostic plots for the fitted growth and survival objects including size range, survival, and life expectancy for Arizona fescue.

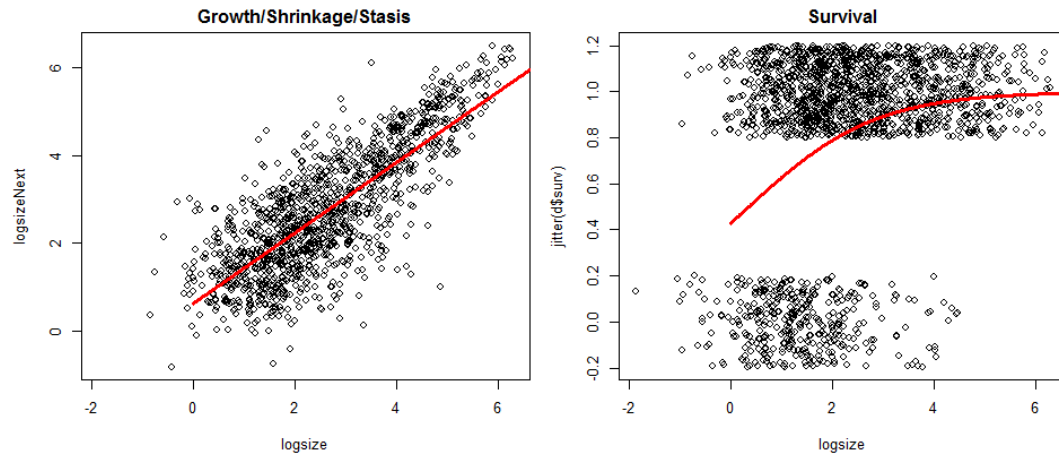


Figure 4.6. The fitted survival and growth functions for Arizona fescue.

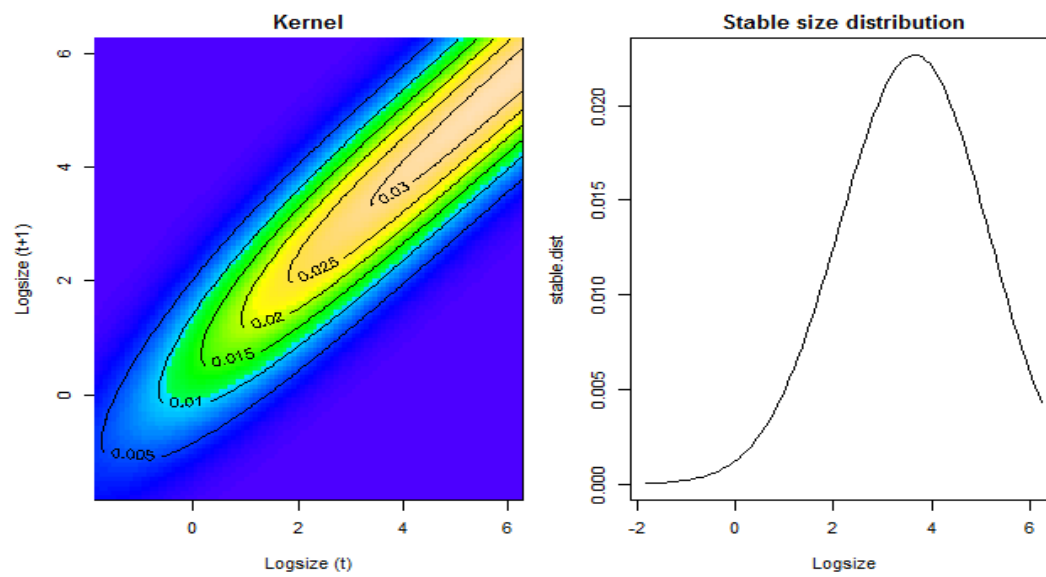


Figure 4.7. The discretized IPM growth kernel and stable size distribution for Arizona fescue using the fitted survival and growth functions from Figure 4.7.

CHAPTER 5:

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

This thesis documents the tremendous value of long-term permanent chart quadrats in providing ecological insights into plant population and community dynamics. The fine-scale resolution of chart quadrat maps allows for spatially explicit tracking of individuals over time, which provides essential demographic information for understanding herbaceous plant communities (Laurenroth and Adler 2008, Zachmann 2010). The spectrum of ecological insights that chart quadrat data can provide today has expanded far beyond what early researchers could have imagined when they first established these historic studies. While contemporary applications are vast, applications of these data will continue to grow over time as science and technology advances and new innovative techniques for data analysis emerge.

In Chapter 2, I combined chart quadrat data from three distinct historical studies into one core dataset that can enable researchers to test ecological theories and describe spatial and temporal species and community patterns in the ponderosa pine-bunchgrass ecosystems of the Southwest (Zachmann 2010, Bakker et al. 2008). Through sharing this rare and valuable ecological dataset with the global scientific community, I hope to inspire agencies and organizations to continue funding the annual mapping of permanent chart quadrats. Unquantifiable value lies in the scientific legacies that we build, and through the maintenance of historic long-term research projects, we can provide opportunities

for future discovery of innovative ecological solutions to unforeseen environmental issues.

In Chapter 3, I introduced an electronic field data collection method for mapping chart quadrats provided evidence that this new method can reduce the total amount of time required to process chart quadrat data by approximately a half an hour per quadrat. Reducing the amount of time and resources needed to remap these permanent chart quadrats annually allows project managers to allocate funding elsewhere in the project budget. I hope to facilitate the annual mapping of this network of permanent chart quadrats by providing a feasible alternative to traditional paper-based methods that can reduce the amount of time and manual labor needed, streamline the field data collection, and improve quality assurance and quality control.

In Chapter 4, I demonstrated that it is feasible to construct Integral Projection Models (IPMs) using data derived from permanent chart quadrats. Using climate variables as covariates, such as precipitation in this study, provides a powerful way to project an individual species' fate over time under different climate change scenarios. IPMs provide scientists with a statistically robust and mechanistically informed method of addressing old but important ecological questions (Merow et al. 2013). Current data collection procedures allow the investigation of factors that limit the growth and survival of plant populations, however, limit the ability of users to examine the effect of climate and land-use practices on their reproductive output. I also recommend exploring non-destructive methods of estimating fecundity so that future users can build an

Fmatrix and utilize *IPMpack*'s full capacities (Metcalf et al. 2014). Dalglish and colleagues (2011) modeled recruitment data at the quadrat-level because field mappers are unable to determine which recruits are produced by potential parent genets.

Although we can currently use these data to provide valuable insights into the survival and growth of individual plant species in response to both fine-scale (i.e., soils, density-dependent competition, tree canopy cover, etc.) and broad-scale (i.e., climate and land-use practices), the absence of fecundity data does limit our ability to derive robust estimates of population growth rates (λ) and conduct sensitivity and elasticity analyses. Modifying the current field procedures to include non-destructive quadrat level measurements of fecundity can allow for future explorations into the reproductive rate for many species without compromising the quality of the data.

Through the use of *IPMpack*, I documented the relationship between winter and spring precipitation and the survival and growth of a dominant perennial bunchgrass, which can be used to inform adaptive management strategies in the Southwest. Since *IPMpack* is designed to allow users to manipulate factors according to specific future climate or land-use scenarios, land-managers can use this specialized tool to predict how target species may respond to the implementation of silvicultural prescriptions or restoration treatments.

The need to develop new and innovative management strategies that are founded in science-based knowledge of ecosystem processes is taking on an

unprecedented level of urgency (Dalglish et al. 2010, Adler et al. 2012). This thesis provides documentation of the value of long-term environmental research in answering historical, contemporary, and future ecological inquiries into the patterns and processes that effect plant community composition and production. Through science-based approaches to predicting shifts in plant populations, which are the result of anthropogenic climate and land-use change, we can attempt to mitigate the impacts of climate change and adapt our land-use practices to restore and conserve native plant populations and communities.

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CHAPTER 7: APPENDICES

Appendix. Table 4.3. Survival and growth models for Arizona fescue. ‘Best fit’ models for survival and growth indicated by lowest AIC and p-value and are in bold.

<i>Festuca arizonica</i>			
Survival	Generalized Linear Models	P-Value	AIC
1	(surv~logsize)	<0.001	1524.1
2	(surv~logsize + winter precipitation)	0.560	1525.8
3	(surv~logsize + spring precipitation)	0.672	1525.9
4	(surv~logsize + monsoonal precipitation)	0.2318	1524.7
5	(surv~logsize + winter precipitation + winter precipitation^2)	<0.001	1477.6
6	(surv~logsize + winter precipitation + spring precipitation)	C1-0.645 C2-0.817	1527.7
7	(surv~logsize + winter precipitation + monsoonal precipitation)	C1-0.475 C3-0.206	1526.2
Growth	Parameters	P-Value	AIC
1	(logsizeNext ~ logsize)	<0.001	3153.6
2	(logsizeNext ~ logsize + winter precipitation)	0.602	3155.4
3	(logsizeNext ~ logsize + spring precipitation)	<0.001	3104.2
4	(logsizeNext ~ logsize + monsoonal precipitation)	<0.001	3119.5
5	(logsizeNext ~ logsize + winter precipitation + winter precipitation^2)	C1-0.0220 C1 ² -0.0249	3152.3
6	(logsizeNext ~ logsize + winter precipitation + spring precipitation)	C1-0.1086 C2-<0.001	3103.2
7	(logsizeNext~logsize + winter precipitation + monsoonal precipitation)	C1-0.090 C3-<0.001	3118.6